Universidade de Lisboa
Faculdade de Medicina de Lisboa

BRAIN AND MOTOR PERFORMANCE: INSIGHTS ON EXERCISE DEPENDENT MOTOR LEARNING, CONSOLIDATION AND INHIBITION ACROSS DIFFERENT TASKS AND LIFE-SPAN

Tiago Miguel Rodrigues Pereira

Orientadores:
Professor Doutor Alexandre Lemos de Castro Caldas
Professora Doutora Ana Maria Blom Vidal Abreu Nelas

Tese especialmente elaborada para obtenção do grau de Doutor em Ciências Biomédicas (ramo Neurociências)

2017

Universidade de Lisboa

Faculdade de Medicina de Lisboa

BRAIN AND MOTOR PERFORMANCE:
INSIGHTS ON EXERCISE DEPENDENT MOTOR LEARNING,
CONSOLIDATION AND INHIBITION ACROSS DIFFERENT TASKS AND LIFE-SPAN

Tiago Miguel Rodrigues Pereira

Orientadores:
Professor Doutor Alexandre Lemos de Castro Caldas
Professora Doutora Ana Maria Blom Vidal Abreu Nelas

Tese especialmente elaborada para obtenção do grau de Doutor em Ciências Biomédicas (ramo Neurociências)

Juri:
Presidente:

- Doutor José Augusto Gamito Melo Cristino, Professor Catedrático e Presidente do Conselho Científico da Faculdade de Medicina de Lisboa

Vogais:

-Doutor João Paulo Vilas Boas Soares de Campo, Professor Catedrático da Faculdade de Desporto da Universidade do Porto;

-Doutor João Manuel da Cunha Silva Abrantes, Professor Catedrático da Universidade Lusófona de Humanidades e Tecnologias;

-Doutor Alexandre Lemos de Castro Caldas, Professor Catedrático do Instituto de Ciências da Saúde da Universidade Católica Portuguesa; (Orientador)

-Doutor Mamede Alves de Carvalho, Professor Catedrático da Faculdade de Medicina da Universidade de Lisboa;

-Doutora Maria Isabel Segurado Pavão Martins Catarino Petiz, Professora Associada com Agregação da Faculdade de Medicina da Universidade de Lisboa;

-Doutor João Nuno Marques Parracho Guerra da Costa, Professor Auxiliar Convidado da Faculdade de Medicina da Universidade de Lisboa

2017

“ A impressão desta tese foi aprovada pelo Conselho Científico da Faculdade de Medicina de Lisboa em reunião de 19 de Fevereiro de 2016.”

Todas as afirmações efectuadas no presente documento são da exclusiva responsabilidade do seu autor, não cabendo qualquer responsabilidade à Faculdade de Medicina de Lisboa pelos conteúdos nele apresentados.

to you, Maria

“If the Human Brain would be so simple that we could understand it,

we would be so simple that we couldn’t”

Emerson M. Pugh

TABLE OF CONTENTS

ACKNOWLEDGEMENTS	**8**
ABBREVIATIONS	**10**
ABSTRACT	**11**
RESUMO	**13**
INTRODUCTION	**17**
FIRST STUDY	**23**
Pereira, T., Abreu, A. M., & Castro-Caldas, A. (2013). Understanding Task-and Expertise-Specific Motor Acquisition and Motor Memory Formation and Consolidation. Perceptual & Motor Skills, 117(1), 108-129.	**23**
SECOND STUDY	**57**
Pereira, T., Castro-Caldas, A., & Abreu, A. M. (2014). Age-related Gender Differences in Motor and Inhibitory Learning and Consolidation. Journal of Advanced Neuroscience Research, 1, 10-21.	**57**
THIRD STUDY	**87**
Pereira, T., Castro-Caldas, A., & Abreu, A. M. (under revision on Scientific Reports). Why Sleep when you can Run: Physical Exercise Accelerates the Consolidation of a Motor Sequence	**87**
FOURTH STUDY	**105**
Pereira, T., Abreu, A. M., & Castro-Caldas, A. (under submission). The Effects of Acute Exercise and Cardiovascular Fitness on a Motor Inhibition Task	**105**
FINAL DISCUSSION	**114**
FINAL CONCLUSIONS	**120**
FUTURE RESEARCH	**121**
REFERENCES	**122**

ACKNOWLEDGEMENTS

To Professor Alexandre Castro Caldas. I know that it probably should not be easy to find a way to cooperate, and mutual understanding from two separate backgrounds like ours. I would not have had the same understanding and curiosity with anyone else and I still remember our first talk during my Master Degree. Thank you so much for having seen a possibility of cooperation. Indeed, it is a fascinating world: that of our brain executing motor tasks. I feel that this world underlies a huge potential that I only realized with some of our informal talks.
Thank you for showing me that I should focus more on the how and less on the why. Your support since the beginning and my inclusion in our discussion group afforded, many times, the debate of ideas and challenges that are a constant on any curious brain. This is definitely not a goodbye, but maybe a beginning of something that developed across these last few years.

To Professor Ana Maria Abreu, a huge “thank you” for the friendship and knowledge all along this path. I realized that going through a Doctorate “is not only rainbows and butterflies, it is compromise that moves us along!” I Love our scientific discussions about the great outdoors and how our brain perceives Nature. No words will never be enough to thank you your dedication to this project. I found it amazing the way you shared your knowledge and motivation about science and about the methods we must use to achieve excellence. Independently if I will achieve it or not, you will always be a reference.

To Professor Francisco Sobral, for having had such a huge role in Sport Sciences, Thank you for guiding me during my first steps in Neurosciences. At some point I felt that I was understanding more about my own body during exercise. I am still here, and the questions grow everyday. And as we all know how important it is, Professor Ana Faro, in my perspective, has had great forward thinking concerning sports sciences and physical education.

To Professor Alexandre Ribeiro that during the first year of my Master's degree shared the fundamentals of basic neuroscience. And only now, do I have the understanding in some of these fundamental questions. Other, are still to explore.

Thanks to Nuno for understanding my need to search the unknown to maintain my brain active. And for constantly reminding me that we must transform our obstacles into opportunities. The support from Oxigénio Inspira-te, LLC was fundamental for the development of this work. With it I kept my mind active, full of sports and colors.

To everyone that on one day or another helped me solve last minute issues: Débora Oliveira, Ana Estevão, Joana Serpa and all INUAF collaborators.

A special thanks to my students, who always believed in my theories even before we started testing them. Part of this PhD was accomplished thanks to you!

It's your simplicity that allows you to share an unconditional love and friendship. Thank you for all the running days we had, because they shed new light on some of the major questions in this PhD. Sorry for the time we lost and thank you for your company during my nights of work. Thank You Blue!

The biggest thanks I send out to my Parents. They are responsible for how great my life developed, for my never-ending curiosity that was stimulated during my early years of life. Thank you for making me what I am now, capable of understanding that the meaning of life, like in science, is more about sharing. Sharing emotions, goals and results.

Finally, I send out all the beautiful words in the world, to describe what we have been through. Raquel and Maria. I know that at some moments in our lives I have had some strange and crazy ideas like going to study neuroscience, but incredibly you are always there by my side, no matter what. All the moments we have will last in our brains, forever, because we may forget what people say or do, but we will never forget how they make us feel.

ABBREVIATIONS

VO2max - Maximal Aerobic Capacity

fMRI - Funcional Magnetic Ressonance Imaging

EEG - ElectroEncephalogram

TMS - Trans Magnetic Stimulation

BDNF - Brain Derived Neurotrophic Factor

M - Mean

SD - Standard Deviation

yrs - Years

sec - Seconds

ms - Miliseconds

mm - Milimeters

cm - Centimeters

CV - Coeficient of Variation

CG - Center of Gravity

IES - Inverse Efficiency Score

RT - Reaction Time

SE - Standard Error

REST - Rest Group

LOW - Low Intensity Group

HIGH - High Intensity Group

FTS - Finger Tapping Sequence

THR - Target Heart Rate

HRmax - Maximum Heart Rate

HRrest - Rest Heart Rate

ABSTRACT

What are the limits of human motor performance? And how can we control our bodies when performing high complexity motor skills? What happens inside an athlete's brain when the athlete surpasses his/her own limits? And, most of all, what transforms such a skill into an automated action that no longer needs attentional focus? Skills initially requiring a high level of concentration, like the acquisition of a novel motor task, become easier to perform, thanks to brain mechanisms that allow us to consolidate motor skills and focus our attention on something else. To address these questions we performed four studies with the following aims and main results:

In the **first study** we analyzed a group of athletes and a group of non-athletes, to shed new light on how the consolidation of motor memories might differ between these two groups and across different tasks. Our findings suggest that differential formation and consolidation processes underlie different motor tasks. Although athletes did not outperform non-athletes on motor memory consolidation, they were more efficient in acquiring novel tasks, perhaps because the required motor schemes might have been anchored on previously acquired ones.

The **second study** focused on the understanding of how the consolidation of a motor task could differ across the life span and how the capacity to react and inhibit a stimulus might change across age-groups. Our results showed us that the influence of both age and sex in task performance and consolidation is to be taken into consideration in order to ameliorate training and potentiate individual capacities while delaying age-related impairments.

In the **third study** we aimed to measure the influence of acute physical exercise on the consolidation of a motor sequence. This investigation shed new light on physical exercise as a strategy to anticipate the enhancement gain with the consolidation of a motor sequence. However, it was clear that this enhancement was only possible when physical exercise was performed at 85% intensity and not with lower intensities.

In the **fourth study** we aimed to investigate the influence of acute physical exercise and cardiovascular fitness on a go/no-go task, to investigate the impact of acute exercise on reaction time and decision-making, very important for planning exercise schedules. We found that acute exercise had no effect on different fitness level groups, however, the higher cardiovascular fitness group had better results on both conditions, in rest and after the acute exercise. Acute Physical exercise, per se, cannot change our capacity to react to a go/no-go task, however, when performed for enough time to enhance our VO2max, better results will be noted.

With these studies, we have brought to light a new understanding of the limitations and possibilities of the process of motor learning (our performance enhancement during the practice of the task) and consolidation (the performance enhancement or stabilization after practice - during the off-line period where we do not train). The consolidation of motor memories is what allows for the amazing beauty of our seemingly effortless movements and gives us the ability to solve motor issues online, as they appear. Although these mechanisms are common to all of us, a motor expert brain is more efficient when controlling and correcting for errors.

Keywords: Motor Learning; Consolidation; Physical Exercise; Inhibition; Life Span

RESUMO

Durante as últimas décadas os níveis de performance motora aumentaram significativamente em quase todas as modalidades desportivas. Todos os anos, os atletas enfrentam novos desafios com gestos motores que são constantemente ultrapassados e que nos fazem questionar o que acontece no cérebro dum atleta que tenta quebrar os seus próprios limites na execução dessas tarefas motoras. Algo que inicialmente requer um alto nível de concentração, é agora mais fácil de executar graças a mecanismos do cérebro que permitem a consolidação das tarefas motoras e a disponibilidade da nossa atenção em novas tarefas. Esta disponibilidade na atenção pode recair sobre a mesma tarefa motora mas de uma forma mais complexa, ou por vezes, numa tarefa cognitiva executada em simultâneo com a tarefa motora. Tendo em conta que o processo de consolidação da aprendizagem motora é a base de todo o trabalho apresentado nesta tese, esperamos que os resultados e discussão dos mesmos possam auxiliar na compreensão deste processo que é extremamente importante nas diferentes abordagens da actividade física, do desporto e da recuperação motora. Apesar de termos utilizado uma abordagem comportamental em todos os estudos, já nos é possível comparar os nossos resultados com os dados obtidos noutras investigações onde foi feita uma análise do cérebro em funcionamento durante a execução de várias tarefas graças às novas tecnologias como a fMRI, EEG, TMS, entre outras.

Estas questões levaram-nos a avançar para um ***primeiro estudo*** onde foi analisado um grupo de atletas e um grupo de não-atletas com o objectivo de compreender se a capacidade de consolidação de memórias motoras pode ser diferente entre estes dois grupos e como essas diferenças podem ser percepcionadas em diferentes tarefas motoras. Os resultados obtidos sugerem que os processos de formação e consolidação subjacentes a diferentes tarefas motoras são também diferentes independentemente do nível de performance. Contudo, embora os atletas não tenham tido uma maior consolidação das tarefas motoras quando comparados com os não-atletas, revelaram uma maior eficiência na aquisição dessas novas tarefas. Esta maior eficiência pode dever-se ao fato dos novos esquemas motores terem sido ancorados noutros esquemas motores previamente adquiridos pelos atletas.

Se por um lado, as novas tecnologias não são totalmente portáteis para serem utilizadas em situação real de exercício físico, por outro, já existem dados de várias investigações nesta

área, com recurso a estas mesmas tecnologias, que nos ajudam a compreender que o exercício físico não resulta apenas da ativação das áreas motoras do cérebro, mas sim de um conjunto mais alargado de redes neuronais. Neste contexto sabemos que os efeitos do exercício físico vão além das habilidades motoras e podem mesmo influenciar outras funções cerebrais ligadas, directa ou indirectamente, à função motora. No entanto, no que diz respeito à aprendizagem de tarefas motoras, ainda há questões que permanecem em aberto, como por exemplo: até que ponto conseguimos melhorar uma aprendizagem motora? Não tendo em conta as limitações anatómicas e biomecânicas, as aprendizagens motoras poderiam continuar a melhorar com um programa de treino suficientemente individualizado e um processo de consolidação altamente controlado. Contudo, tendo em consideração que a aprendizagem motora está dependente dos nossos músculos e de outras funções periféricas, é fundamental clarificarmos a forma como a consolidação destas aprendizagens interage com as diferentes variáveis e como a conseguimos integrar nos planos de treino, de maneira a melhorar e optimizar a performance motora. Esta melhoria da performance motora através de planos de treino optimizados pode ter especial importância num atleta ou mesmo em pessoas em fase de recuperação motora.

Com o envelhecimento da população humana e consequente aumento das limitações motoras, são necessárias melhores estratégias para que possamos aumentar a qualidade de vida da população idosa e o exercício físico pode constituir uma peça fundamental neste processo para se envelhecer de forma saudável. No seguimento desta ideia, o ***segundo estudo*** centrou-se na compreensão de como a consolidação de uma tarefa motora poderia variar ao longo da vida e simultaneamente perceber como a capacidade de reacção e inibição motora pode mudar em diferentes grupos etários. Os resultados obtidos revelaram-nos que a idade e o sexo têm influência na aprendizagem, consolidação e inibição de tarefas motoras. Estes dados levam-nos a considerar estas variáveis da aprendizagem motora como fundamentais na análise e construção da aprendizagem geral, potenciando a aquisição e consolidação das capacidades individuais como forma de diminuir as performances mais baixas relacionadas com o envelhecimento.

Para além das considerações anteriores, quando aprendemos um gesto motor há sempre algum tipo de esforço físico associado. No entanto, apesar deste esforço poder apresentar intensidades diferentes, devemos analisar este esforço físico como um potencial interveniente na aprendizagem de uma tarefa motora, principalmente quando se trata de uma sequência motora, em que o nível de integração e consolidação é superior comparativamente a gestos motores mais simples. Considerando que as nossas investigações anteriores demonstraram um efeito positivo na aprendizagem motora, que pode de alguma forma estar relacionado com o processo de consolidação ao nível cerebral, o nosso ***terceiro estudo*** incidiu sobre a influência do exercício físico agudo na consolidação de uma sequência de motora. Foram utilizados grupos com diferentes intensidades, que desenvolveram uma única sessão de exercício físico após a aprendizagem de uma sequência motora. Esta investigação veio clarificar a acção do exercício físico como meio para potenciar os ganhos na performance motora, sem treino adicional, através da consolidação em sequências motoras. No entanto, nos nossos resultados, ficou demonstrado que este aumento só foi possível quando o exercício físico é realizado com uma intensidade de 85% e não nas intensidades mais baixas.

Este terceiro estudo foi complementado com uma quarta investigação onde explorámos o exercício físico como variável interveniente numa função cerebral extremamente importante em actividade física: A tomada de decisão e o seu tempo de reacção. Desta forma, o ***quarto estudo*** teve como objetivo investigar a influência do exercício físico agudo e a capacidade cardiovascular numa tarefa go / no-go. De acordo com investigações anteriores, uma única sessão de exercício físico pode promover mudanças em algumas das nossas funções cerebrais, contudo estes resultados não representam os efeitos a longo prazo do exercício físico. Nesse sentido, utilizámos dois grupos com diferentes níveis de capacidade cardiovascular em que ambos executaram uma tarefa go / no-go em duas situações distintas: em repouso e após o exercício físico agudo. Ao fazermos uma análise aos dois grupos com diferentes capacidades cardiovasculares, tivemos a possibilidade de analisar os efeitos do exercício físico a longo prazo no desempenho da tarefa. Os resultados obtidos demonstraram que o exercício físico agudo não teve qualquer efeito nos resultados da tarefa em nenhum dos grupos. No entanto, o grupo com maior capacidade cardiovascular obteve melhores resultados na tarefa go / no-go em ambas as condições, em repouso e após o exercício agudo. O exercício físico agudo, por si só não alterou a capacidade para reagir a uma tarefa motora, no entanto, quando desenvolvido por tempo suficiente para melhorar as nossas capacidades cardiovasculares (melhores resultados de VO2máx) as melhorias na performance da tarefa go / no go foram notadas.

Através da realização destas investigações e a compilação nesta tese, esperamos que, os resultados obtidos, possam contribuir, para uma melhor compreensão das limitações e possibilidades do processo de aprendizagem motora (melhoria de desempenho durante a prática da tarefa) e do processo de consolidação (a melhoria de desempenho ou de estabilização após a prática - durante o período off-line). A consolidação de aprendizagens motoras permite-nos alcançar uma melhor performance na execução dos nossos movimentos com um menor esforço muscular e que aparentemente torna mais fácil a resolução de problemas motores. Esta situação acontece frequentemente no nosso dia-a-dia, no entanto, um cérebro com uma maior especialização motora consegue ser mais eficiente no que diz respeito ao controlo e correção de erros.

INTRODUCTION

Motor Learning and Consolidation

The motor skills present in our daily lives, like riding a bike, writing a text, playing music or swimming are all acquired by practice. With time, these skills tend to be performed more quickly and accurately (Dudai, 2004). Since birth, we challenge ourselves to learn new motor skills, and when we arrive to an older age, we have an added challenge of not loosing some of the skills we have learned throughout life. Some of these skills or motor tasks may seem easy to perform, but the fact is that our brain will work with several of its structures, like the motor cortex, hippocampus, basal ganglia and most of sensory areas and peripheral receptors (Cross et al., 2007) to perfectly perform a motor task. It is easy to understand that a motor task will become more efficient with practice and that some of our motor skills will last for many years. However, the consolidation process of motor memories is far from being totally understood and it does not happen only during the effective practice of the task. In accordance to this, a few years ago, Walker and collaborators (2002) reported a significant enhancement on motor performance 24 hours after a training session without additional training. The authors attributed the responsibility of this enhancement to a nights' sleep between the training session and the re-test, 24 hours after training. Since then, much research has been done to clarify the role of sleep in the consolidation of motor memories, either on a behavioral level (Debarnot et al., 2011 Walker, 2005; Fischer et al., 2005;), or concerning the molecular processes and networks behind this enhancement without additional training (for review see Abel, et al., 2013). Nevertheless, other studies, have also suggested that post-sleep performance enhancement is not dependent on sleep and might be related with the design of the protocols (Cai & Rickard, 2009). Be it dependent on sleep or not, performance enhancement has been widely reported when a motor task is re-tested a few hours after the initial training session and these changes have been associated to brain plasticity occurring during the off-line period (period after practice) (Debas et. al., 2010). For this reason, every time we learn a new motor task, the performance that should be considered should be the one after the consolidation period, as we continue to improve after the training session - but with different consolidation processes for different motor tasks (Pereira et al., 2013).

The learning of motor skills initially develops relatively fast (with fast improvements on performance) and more slowly in later phases, when one needs more time to enhance performance (Doyon & Benali, 2005). These two learning phases are called: fast and slow learning, respectively. Nevertheless, it is important to have in mind that for different tasks, the duration of the fast and slow phases can be completely different. For example: the fast learning phase on a simple finger tapping sequence can last minutes and, the fast learning phase of a complex sport skill can last months. The off-line enhancement we described above occurs between these two phases (Dayan & Cohen, 2011) and is dependent on the physiological and structural synaptic changes that will allow a motor memory to consolidate, due to protein synthesis and changes in synaptic morphology that potentiates long lasting molecular changes (Dubai, 2006; Dayan & Cohen, 2011). The structural changes on a system level are dependent on the cerebellum, basal ganglia and hippocampus (Doyon et al., 2009) and a recent research (Albouy et al., 2013) showed a great interaction between the striatum, the hippocampus and prefrontal cortex systems as a way to predict the consolidation of motor memory during the off-line period. With all these implications of the off-line enhancement of performance, it is very important to find the best structure for training plans and understand if there might be any differences between populations with different expertise levels.

In addition to this, the fact that we can also experience a motor performance enhancement as result of imagery or mental training of a task (Debarnot et al., 2010) is also of extreme importance when considering the best strategy to apply in face of individual motor limitations due to injury, or even to complement the daily motor training plans. If we learn the most correct training strategy for each motor sequence or for a number of motor processes, we will potentiate and optimize motor learning. Mental training can even enhance cognitive processes and is not task-specific (Slagter et al., 2011), which can be positive in some situations like team sports where the requirements for success go beyond the correct performance of a motor skill.

Motor learning and inhibition

Understanding motor memory consolidation will help us improve motor learning across different tasks, in different times of life and also to integrate different tasks on the same training plan. The idea that a similar task could help us learn a novel motor task is no longer accepted, as we now have evidence that, the practice of similar tasks is not necessarily better on the transfer of motor movements (Boutin et al., 2012). Once we consolidate a motor memory, with all the practice and training across that process, the inhibition of that motor memory is essential to create a new one, but will always be more difficult due to the fact that the learned task is automatized. In addition, we also know that even a single session of exercise can affect the inhibition of a motor response by having a selective effect, increasing the attentional resources (Chu et al., 2015). This increase in attentional resources can help us to understand the mechanisms behind inhibitory tasks and the capacity to enhance performance when we need to inhibit previously learned task, to learn a new motor sequence. However, we must not forget that some of the motor tasks are being learned during physical exercise, and despite the fact that exercise does not influence the executive processing tasks, the arousal promoted by exercise facilitates the sensory processes involved in stimulus detection (Lambourne et al., 2010) and can help to understand how a motor inhibition task is enhanced.

The study of inhibition on motor learning is extremely important because, in sports, as well as in many other motor action programs we participate in throughout life, we are constantly making motor decisions based on a go/ no-go interaction. Saying this, we can look at athletes as experts in motor decision-making. It is important to study the decision-making process present on motor memory consolidation across different ages (as we mentioned above), but we should also look into the inhibitory processes that might arise due to the interference of physical exercise.

Why is the athlete's brain different?

In the early years of brain research, most of the discoveries were made on post mortem brains, and were based detected behavioral disfunctions that were associated to brain lesions (Lashley, 1950). Nowadays, with the material resources we have available, like, fMRI, EEG or molecular analysis, we are now, more than ever, able to look into our live brain while working. We can analyze our brain while we are learning a task, having a social behavior or dealing with several emotions and this leads to a whole new world of possibilities in what pertains to the understanding of our brain functions. Taking into consideration that the priority, in terms of research, concerns fighting brain diseases, most research uses protocols and subjects that suffer from a specific disease where one can investigate an abnormal, sick or lesioned brain. However, it is important to consider that there are individuals (on the opposing side of a pathological condition) that pushed their brains to the limit of motor control and learning. The brain model of an athlete, or someone who has been exposed to a high level of brain changes through physical exercise or motor learning, can be used to predict and plan the goals to achieve and structure of the training sessions. In addition to this, it is possible that all the studies in this field should use physical active people as controls, instead of sedentary people, since our active brain is a result of a series of factors wherein regular physical activity habits should be included. Of all the outstanding skills in athletes, we highlight the forward models, referred as the capacity to predict our or other body actions a few moments before they happen (for review see Yarrow et al., 2009). With forward models, our brain can estimate a precise action of a body part or an object even before the arrival of sensory feedback (Wagner et al., 2008). If we consider that forward models can be trained and athletes are an excellent example of how to train them, we might potentiate the learning of a motor task through this and develop a better model of motor learning and consolidation across the population. There is still a long way to go, until we get a clear understanding of how this system works in detail and how it changes from athletes to non-athletes, across our life-span or even between different motor tasks. For this reason here we shed new light on this issue and propose a research that connects different expertise groups, different ages and different tasks, in order to avoid a biased generalization of results.

Physical exercise, motor learning and consolidation

When we train our aerobic performance to achieve better physical fitness, we can use a training plan that includes a series of individual sessions where the effect of supercompensation is present (Gambetta, 2007). Supercompensation refers to the bodies' subsequent adaptation to stress in order to maintain homeostasis in our energy systems that will enhance the energy production performance (Gambetta, 2007) and our metabolism will be more efficient next time we perform that same physical exercise. This adaptation, results from a training charge to our physiology and increases from session to session. The effects of physical exercise on muscle and energy systems and their molecular basis are not new (Robergs et al., 2004), however, it is also known that they can have different efficiencies across life (for review see Voss et al., 2011) and across individuals with different physical fitness levels (VO2max). This evidence has been used for a long time to design training plans for athletes and people going through motor recovery but only recently have we had some research that brought new light on the effects of physical activity and exercise on brain function (for review see Thomas et al., 2012). We have now more insights to better understand the effects of physical activity and exercise on a central perspective that complements the previous research on the peripheral effects. Subtending the occurrence of a muscle contraction and energy production, our motor cortex plays an important role during exercise (Peterson et al., 2012) and the M1 area is particularly active during physical activity.

Motor Learning Across Life

Independently of our age, we are constantly learning or adapting motor skills, but older adults represent motor sequences differently than younger adults Panzer and Colaborators (2011). Nevertheless, a motor skill is more efficient when we can achieve the best motor performance with the lowest energy expenditure. So, our motor learning tasks are always connected with our muscle and energy system. The differences about our muscles, energy production and optimization across life have been widely studied (for review see Voss et al., 2011) but we need more research to better understand the learning and consolidation of motor tasks across life. Such future research will enable us to connect central and peripheral data on motor learning and consolidation across our life. Several studies with young adults have reported that motor performance is enhanced after a training session, during the off-line period (Krakauer & Shadmehr, 2006). However we need to understand if this enhancement is maintained across life. Moreover, it is important to ask if children will have different consolidation performances compared to young adults, mature adults, or older adults. Previous investigations showed differences between children and adolescents on a motor learning task (Dorfberger et al., 2007) that might be related to a less selective process during childhood that becomes more selective with age. This may justify the idea that children are more permeable to learning novel movements. Nevertheless,, according to the same authors, the consolidation of these new movements is not as effective as it is in young adults. Together with young adults, one of the most investigated groups in what concerns the determination of the effects of physical activity on cognition and brain function, is the older population, mostly because of the newest possibilities for exercise that might help prevent age-related cognitive decline and neurodegenerative diseases (Bherer et al., 2013). However, recently a new idea came up, suggesting that physical exercise can only reduce dementia, cognitive decline and other aging limitations, when practiced for a long time period (Ahlskog et al., 2011). At this moment we are not able to confirm this or other theories that correlate physical activity and aging, because most research does not consider a longitudinal approach and the results with a significant positive effect between aging and physical activity are recent. We need more studies to understand how the effects of motor learning and/or physical exercise can be extended in time and what is the behavior of a performance curve. Taking into consideration that, aerobic exercise can be used to improve cognition and motor function posts-stroke (Quaney et al., 2009), long term protocols should be established for everyone in order to engage in a healthy aging process, so that we might shed new light on the positive effects of motor learning and physical exercise, not only in older adults, but also, across the life span.

FIRST STUDY

Pereira, T., Abreu, A. M., & Castro-Caldas, A. (2013). Understanding Task-and Expertise-Specific Motor Acquisition and Motor Memory Formation and Consolidation. Perceptual & Motor Skills, 117(1), 108-129.

Perceptual and Motor Skills

Understanding Task-and Expertise-Specific Motor Acquisition and Motor Memory Formation and Consolidation[1,2,3]

TIAGO PEREIRA
Institute of Health Sciences, Portuguese Catholic University, Lisbon, Portugal
Laboratory of Physical Activity and Health, Instituto Superior Dom Afonso III, Loulé, Portugal

ANA MARIA ABREU
Faculty of Human Kinetics, Technical University of Lisbon, Portugal

ALEXANDRE CASTRO-CALDAS
Institute of Health Sciences, Portuguese Catholic University, Lisbon, Portugal

---

[1] Address correspondence to Ana Maria Abreu, Laboratory of Expertise in Sports, Faculty of Human Kinetics, Technical University of Lisbon, Estrada da Costa, 1495-688 Cruz Quebrada, Portugal or e-mail (amabreu@fmh.utl.pt).

[2] TP acknowledges the *Instituto Superior Dom Afonso III* for allowing the use of University space to develop this research. This work was supported in part by a postdoctoral grant SFRH / BPD / 36350 / 2007 from the *Fundação para a Ciência e Tecnologia* of Portugal to AMA.

[3] This study was presented as a poster at the European Workshop on Movement Science (EWOMS'09).

Summary. This study aimed to assess how the capacity to acquire, form and consolidate motor memories might vary across different tasks and different groups (with and without motor expertise). We tested 20 athletes and 21 non-athletes in five motor tasks: a motor sequence task, a reaction time task, two visuo-manual tasks, and a balance task. Performance was measured before training (T0), immediately after training (T1), and 24 hours after training (T2), to assess motor memory acquisition, formation and consolidation. T2 performance was higher in both groups, without additional training, on the motor sequence task, reaction time task and only one of the visuo-manual tasks (pouring task). Athletes had better baseline performance at T0 than non-athletes on these tasks. Findings suggest that differential formation and consolidation processes underlie different motor tasks. Although athletes did not outperform non-athletes on motor memory consolidation, they were more efficient in acquiring novel tasks, perhaps because the required motor schemes might have been anchored on previously acquired ones.

Introduction

Recent scientific research on sports and neuroscience has provided evidence for the importance of developing optimal training plans in order to ameliorate the motor performance in every training session. Williams, Ward, Knowles and Smeeton (2002) showed that perceptual training, for example, improved anticipation skills in tennis. Dishman, Berthoud, Booth, Cotman, Edgerton, Fleshner, Gandevia, Gomez-Pinilla, Greenwood, Hillman, Kramer, Levin, Moran, Russo-Neustadt, Salamone, Van Hoomissen, Wade, York and Zigmond (2006), on the other hand, show that motor skill training and voluntary physical activity lead to numerous neuroplasticity benefits that, in turn, enhance cognitive functions and some types of learning, such as motor learning. Further research has provided evidence for the importance of training programs for people undergoing motor recovery from brain lesion or disease (Starr, Leaper, Murray, Lemmon, Staff, Deary, & Whalley, 2009; Albouy, Sterpenich, Balteau, Vandewalle, Desseilles, Dang-Vu, Darsaudi, Ruby, Luppi, Degueldre, Peigneux, Luxen, & Maquet, 2008). The success of training programs should depend on capacity to consolidate motor memories, as consolidation of motor memories implies a number of conditions under which the neural substrate resists to disruption (for review, see Krakauer & Shadmehr, 2006). Recalling a motor scheme from motor memories may be manifest as the correct movements for executing a certain task. This recall is possible after the consolidation of motor memories has occurred (i.e., a set of stages that a motor memory undergoes to become more stable with the passage of time (Criscimagna-Hemminger & Shadmehr, 2008). Consolidating motor memories is especially useful when more than one novel movement or a series of complex novel movements are learned in a training session. In a passive observation fMRI study, Calvo-Merino, Glaser, Grèzes, Passingham and Haggard (2005) showed that a neural system with mirror properties integrates observed actions of others with one's own personal motor repertoire, suggesting that the human brain understands actions by motor simulation. It thus follows that certain actions may figure in the motor repertoire of a trained expert but not in the motor repertoire of a non-athlete (someone who has not undergone motor training). Researchers have sought to investigate the impact of motor expertise on neural plasticity in groups of experts such as athletes (e.g., Aglioti, Cesari, Romani, & Urgesi, 2008) or musicians (e.g. Hyde, Lerch, Norton, Forgeard, Winner, Evans, & Schlaug, 2009; Tervaniemi, 2009). Brain plasticity, i.e., the brains capacity to change and reorganize its neural networks, occurs after learning a motor task, not only in motor areas, but also in other networks. Filippi, Ceccarelli, Pagani, Gatti, Rossi, Stefanelli, Falini, Comi, and Rocca (2010) and Ostry, Darainy, Mattar, Wong and Gribble (2010) state that such motor plasticity persists for long periods of time. Together, these studies show that both structural and functional neural changes occur with motor learning. When learning leads to expertise, additional expert-specific changes might occur, such as the activation of error-detection areas during the visualization of motor action scenes in the domain of the athlete's expertise (Abreu, Macaluso, Azevedo, Cesari, Urgesi, & Aglioti, 2012) (for a comprehensive review on the neuropsychology of high achievement in sports see Yarrow, Brown, and Krakauer (2009)).

With imaging techniques, the function of athlete´s brain has been the object of study. Higher blood flow in the primary motor cortex areas has been associated with motor expertise (Brisswalter, Collardeau, & René, 2002; Hutchinson, Lee, Gaab, & Schlaug, 2003; Watson, 2006) as well as the occurrence of plasticity phenomena (Park, Lee, Han, Lee, Lee, Park, & Rhyu, (2009); Russmann, Lamy, Shamim, Meunier, & Hallett, 2009). These researchers report the neural and behavioral consequences of motor expertise. However, to become an expert at a given motor skill (such as those needed for sports), one first needs to learn that skill and consolidate the respective motor memories. Motor memory consolidation should lead to better motor performance. The purpose of this research is to investigate the process of motor memory consolidation. According to Wei and Luo (2010) sports expertise and associated plasticity are task specific. The aim of this research is to shed new light on how the specificity of expertise and plasticity might differentially influence the acquisition, memory formation and consolidation of new motor tasks and how this might relate to different groups (with and without specific motor expertise). The present research thus opens a new window of intervention (i.e. by understanding motor memory consolidation, one might create optimal consolidation conditions that, in turn, should lead to the development of better motor performance and ultimately, motor expertise) and hopefully contributes to the optimization of coaching techniques. Corollary to this are the reports by several authors (Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002; Baraduc, Lang, Rothwell, & Wolpert, 2004; Wu, Kansaku, & Hallet, 2004; Fisher, Nitschke, Melchert, Erdmann, & Born, 2005) suggesting that, after learning a task, motor memories undergo a transformation associated to a neural reorganization leading to better performances without additional training. This performance enhancement after consolidation could be dependent on overnight sleep (Walker, Brakefield, Hobson, & Stickgold, 2003; Walker & Stickgold, 2005; Kuriyama, Stickgold, & Walker, 2004). Alternatively, according to other authors (Rickard, Cai, Rieth, Jones, & Ard, 2008; Cai, & Rickard, 2009) sleep is not a factor for motor performance enhancement. Others still, state that consolidation might be initiated during a waking period. With learning, this process might be extended to sleep (e.g. Vertes, 2004). Independently of the quantity and quality of sleep on motor memory consolidation processes, these authors seem to agree, however, with a simple model view of the issue. This has been reflected, for example, on the generalization of the gains on performance on one task to other motor tasks. Research on motor memory consolidation has been based on a one-task paradigm (i.e., if one obtains better performance after consolidation on a certain task, then this performance gain will serve as an indication of a generalized performance gain for other motor tasks, independently of some differences between them).A single task is not likely to represent or encompass the variability of human motor movements. Different motor tasks might undergo different consolidation processes: Krakauer (2009) has described specific forms of visuo motor learning; Lalazar and Vaadia (2008) have investigated the neural bases of sensorimotor learning and Smyth, Summers and Garry (2010) have explored how specific primary motor activation might be associated to differences in motor learning success. Moreover, not all physical activities and sports are similar, and the consequences on neural activity of expertise on different action schemes might also differ as it does with musicians, as reviewed by Tervaniemi (2009). Success of performance in sports might depend mainly on the physical condition of the participant. Dishman, Berthoud, Booth, Cotman, Edgerton, Fleshner, Gandevia, Gomez-Pinilla, Greenwood, Hillman, Kramer, Levin, Moran, Russo-Neustadt, Salamone, Van Hoomissen, Wade, York, and Zigmond (2006) state that physical condition can positively impact on performance of cognitive tasks across the lifespan and even more so for those processes related to acquiring greater executive control (i.e., processes involved in scheduling, planning, monitoring, and task coordination). Some researchers (Abbott, White, Ross, Masaki, Curb, & Petrovich, 2004; Eggermont, Swaab, Luiten, & Scherder, 2005; Larson, Wang, Bowen, McCormick, Teri, Crane, Kukull, 2006) also report a reduction in the risk of neurodegenerative diseases, associated to a good physical condition. These reported benefits of physical activity on brain function, are commonly associated with the improvement in neurothrophic brain factors like the enhancement of serum levels of BDNF after acute exercise regimens (Ferris, Williams, & Shen, 2007) that are not present on non- active people (henceforth non-athletes) (Scherder, Van Paasschen, Deijen, Knokke, Orlebeke, Burgers, Devriese, Swaab, Sergeant, 2005; Winter, Breitenstein, Mooren, Voelker, Fobker, Lechtermann, Krueger, Fromme, Korsukewitz, Floel, Knecht, 2007). Moreover, these benefits have been associated with chronic practice of sports where performance is dependent on physical condition. In other cases, success might depend on mastering a technique (i.e. motor scheme). However, most sports require both physical condition and mastering the movements that constitute the required action scheme. In this study, a sport (gymnastics) is investigated. Gymnastics was chosen because performance is not only dependent on physical condition, but also, dependent on heightened control of motor actions and on constant adaptations to the complex changes in movement throughout the execution of intricate motor schemes.

If indeed, new motor schemes are anchored on pre-existing ones, than, the neural consolidation process that allows for memory organization after learning should be different in experts and non-athletes. Here, it is suggested that, in expert Athletes, where sport success depends not only on physical condition, but also on high motor control, the constant buildup of new complex motor memories might have consequences for the neural consolidation systems (*for review see* Krakauer & Shadmehr, 2006). Moreover, the constant use of motor memories contributes to brain plasticity. This was demonstrated in animal motor skill learning (e.g., Costa, Cohen, & Nicolelis, 2004) and in fMRI studies with humans (e.g., Olson, Rao, Moore, Wang, Detre, & Aguirre, 2006). These fine-tuned neural systems should reinforce a learning-consolidation feedforward model (Yarrow, Brown, Krakauer, 2009). Both plasticity and coupling phenomena (between consolidated motor memories and newly learned motor schemes) might lead to a facilitation of consolidation. According to this, it is possible that different consolidation processes subtend different tasks, depending on motor complexity overlaps between the learner's experience and the task to be learned.

Hence, it is hypothesized here that motor memory consolidation should lead to better performance at T2 by Athletes than Non-Athletes. Such an improvement in performance with consolidation should result from new memories that might be anchored on, or share some motor plans from, previously acquired motor schemes. Moreover, it is proposed that these previously acquired motor schemes might contribute differently to the consolidation of new motor memories depending on the nature of these schemes (how similar they are to the previously learned motor schemes). Such findings might question the single task paradigm used in motor memory consolidation research thus far.

If one considers what can be learned from differences in performance in acquisition and memory formation phases of motor learning, as well as the consolidation of these memories, one can certainly accept that there are neural underpinnings to these specificities. Recent studies on Brain cognition have been shedding new light on the links between motor learning and brain activity (e.g., Ostry, Darainy, Mattar, Wong, & Gribble, 2010; Smyth, Summers, & Garry, 2010; Tomassini, Jbabdi, Kincses, Bosnell, Douaud, Pozzilli, Matthews, & Johansen-Berg, 2010).

To tackle the issues described above, we used five different motor tasks which tap different aspects of motor schemes (sequence learning, reaction time, visuomanual coordination and balance), to assess motor memory consolidation in a group of elite gymnasts (competing at a national level at the Portuguese Federation of Trampoline and Acrobatic Sports and training at least 5 days per week) and a group of Non-Athletes (without any oriented training in sports).

Methods

Participants

Twenty elite gymnastics experts (athletes -12 male, 8 female) were selected from a National gymnastics team, with an age raging from 16 to 30 years (M = 18.6 yrs., SD = 3.18), and 21 participants with no experience in gymnastics (non-athletes – 9 male, 12 female) were recruited from the University Campus, with an age ranging from 16 to 28 years (M = 22.6 yrs, SD = 3.4). The expert athletes were recruited from a sports club of the Portuguese Federation of Trampoline and Acrobatic Sports (Federação Portuguesa de Trampolins e Desportos Acrobáticos). These Athletes trained five days per week and had practiced gymnastics for a mean of 7.3 years (SD= 3.5). All participants were right handed and had normal to corrected-to-normal vision and no past motor or nervous lesions or disease. Observed power of sample sizes (post-hoc analysis) was calculated using G*Power 3.1; and was very high (Power = 1 – β error probability = 0.9409469).

Measures

All participants were asked to learn and perform five different motor tasks to assess motor memory consolidation. These tasks were novel to all participants and tapped different aspects of motor movement: Finger Tapping Sequence (motor sequencing); Reaction Time (time response to visual stimuli); Circuit Trail and Pouring Tasks (oculomanual integration) and Balance (body adaptations to the instability of the center of gravity). The tasks were chosen because they are simple and representative of motor sequence, reaction time, visuomanual and balance tasks, respectively. A thorough description of the tasks and specific units of measurement is given in the 'Tasks' section.

Procedure

Before inclusion in this study, written informed consent was obtained from all participants and from the participants' parents or guardians, in the case of minors. This study was conducted in accordance with the tenets of the Declaration of Helsinki (1964).

The procedures described below for the motor sequence task were the same as those described by Walker, Brakefield, Morgan, Hobson and Stickgold (2002). Conversely, for the visuomanual task (pouring task), the same protocol as that described by Cavaco, Anderson, Allen, Castro-Caldas and Damásio (2004) was used. The number of training blocks was adapted in the reaction time task protocol, to fit the protocol from the other tasks. If the hypothesis that - athletes should be more proficient at learning novel tasks that share motor schemes with previously learned ones - is correct, then expert gymnasts should perform better at a balance task. Thus, the protocols mentioned above, already described in the literature, were adapted to two novel tasks (circuit trail and balance tasks). Consequently, all tasks ended up with similar training times between them (≈30 sec) throughout 6 blocks of 5 trials and 30 sec rest periods between blocks. By controlling the amount of time spent on acquisition and practice one might infer that the differences thus obtained pertain to the specificities of the task and/or to the specificities of the participant.

These five different tasks were performed (in the following order: Finger Tapping Sequence; Reaction Time Task; Circuit Trail; Pouring Task; Balance Task) in a Training Session (T0 to T1). During this session, Base Line Performance – T0 (first time the task is executed) and Performance After Training – T1 (mean of the last trials (±ri) was measured – the number of trials varied across tasks as described in the 'Tasks' section). Subsequently, all participants were re-tested at the same tasks, after a 24-hour delay (Consolidation Session –T2). The 24-hour period without additional training, allowed for consolidation, is consistent with previous designs (e.g., Krakauer & Shadmehr, 2006). Participants were tested in a silent and poorly lit room (just enough lighting to avoid reflected glare on the computer screen – used in two of the tasks) with the fewest distractors possible. The participants were instructed to have a good night´s sleep (8 to 9 hours) before T2. All subjects met this inclusion criterion. Further description of specific task procedures can be found below in the 'Tasks' section.

Tasks

Task 1 - finger tapping sequence (motor sequences).

Participants were required to learn the following finger tapping sequence: 1_3_2_4_2, by using a regular computer keyboard. The right hand was placed on the keyboard. The fingers corresponded to computer keys as follows: digit 1 – Index finger; digit 2 – Middle finger; digit 3 – Ring finger; digit 4 – Little finger (see Fig.1a). Participants repeated the sequence as quickly and as accurately as possible for 30 sec. Performance was measured by the number of correctly typed sequences. The training session consisted of 12 blocks of 30 sec, with 30 sec rest periods between each block (Kuryiama, Stickgold, & Walker, 2004). During these 30 sec blocks, each subject executed the most amount of trials as possible. Performance (number of correct trials) in the first block of the training session served as T0, whereas the mean score from the last 3 blocks of this session was used as T1. The consolidation session consisted of 3 blocks of 30 sec with 30 sec rest periods between each block. T2 was the mean number of trials executed during all 3 blocks of 30 sec in the consolidation session. The sequences (trials) were recorded online, on the computer during the experiment. On this task, the higher the score (number of trials), the better the performance.

Task 2 - reaction time (time response to visual stimuli).

On this task participants responded to a visual stimulus, presented on a computer screen during 1000 ms, by pressing the space bar on a computer keyboard. The visual stimulus was a stoplight sign (15 mm x 30 mm rectangular box) with three vertically placed colored circles (7 mm diameter each), red on top, yellow in the middle, and green in the bottom (see Fig.1b). At the start of the trial, the red light would be on. Participants pressed the space bar when the light would switch from red to green. Between trials, the yellow dot in the middle would be on. The time taken to switch from red to green was random and could vary between 2 and 7 sec.. The software program was built using a JavaScript code. Performance was measured as reaction time in miliseconds (msec).

The training session consisted of 6 blocks of 5 trials each. T0 was the mean of the first block of trials of the training session (5 trials), whereas the mean scores from the final block of trials were taken as T1 (5 trials). The consolidation session consisted of only 1 block of 5 trials. T2 was the mean for all 5 trials in this session. Reaction times and means for each of these blocks were recorded on the computer. In this task, the higher the score, the poorer the performance.

Task 3 - circuit trail (oculomanual task).

Participants navigate an electric circuit trail with a nuclear metal ring (which encircled the circuit), as quickly and as accurately as possible. The apparatus consisted of an iron circuit with a 65 cm linear path and 9 changes in direction (changes in direction were always vertical – upwards or downwards, never sideways and the circuit trial should be executed from right to left). The metal ring's diameter was 1.5 cm, and it encircled the iron circuit path (see Fig.1c). Task performance was the time taken to navigate through the circuit (speed). For each error committed, 3 seconds were added to the performance score (accuracy). An error was accounted for every time the ring touched the metal trail, signaled by a "bip" sound.

The Training Session consisted of 12 blocks of 1 single trial each with 30 sec rest between trials. T0 was the performance from trial 1 of the training session, whereas T1 was the mean on the last final 3 trials in Block 12. The consolidation session consisted of 3 blocks of 1 single trial each with 30 sec rest between trials. T2 was the mean of all 3 blocks of 1 single trial in the consolidation session. This protocol was similar to the one used for task 1 (Finger Tapping Sequence). Also, in this task, the higher the score, the poorer the performance.

Task 4 - pouring task (oculomanual task).

Participants filled 8 glass cylinders with 20 ml of water each as quickly and accurately as possible. The apparatus included one container with water with an opening of 7 mm diameter and eight graduated cylinders with a diameter of 2 cm each. The eight cylinders rested on a plastic frame (60 cm x 40 cm x 30 cm) with a wire barrier 20 cm above the cylinders to prevent water being poured using a closer distance. On each cylinder was a black line to indicate the 20 ml mark (see Fig.1d). Performance was the time taken to fill all 8 cylinders with 20 ml of water each.

The training session consisted of 6 trials with 30 sec intervals between them. T0 was the score on trial 1 of the training session, whereas T1 was given by the mean score on the final 2 trials. The consolidation session was based on 2 trials with 30 sec intervals between them. T2 was the mean on the 2 trials in this session. This task was adapted from previous research by Cavaco, Anderson, Allen, Castro-Caldas and Damásio (2004). In this task, the higher the score, the poorer the performance.

Task 5 - balance task (body adaptations to instability of the center of gravity).

Participants were asked to stand on a balance platform (a ball platform) during 30 sec and to readjust the body changes created by the instability of the platform. This instability was created by the round base of the platform and diminished by body muscular adaptations. The apparatus was a Fitterfirst disc (USA Patent: 5.810.703) with 40.6 cm of diameter, a quarter round base with 13cm diameter, 5 cm high from ground (see Fig.1e). Performance score was the number of errors on each 30 sec trial. An error was assessed every time the outside of the platform touched the floor (representing maximum instability).

On the training session were 12 blocks of 30 sec trials with 30 sec rest between trials. T0 was performance on trial 1 of the session, whereas T1 was given by the mean score of the final 3 trials. The consolidation session were 3 blocks of 30 sec trials with 30 sec rest between trials. T2 was the mean for all 3 blocks of 30 sec trials in consolidation session.

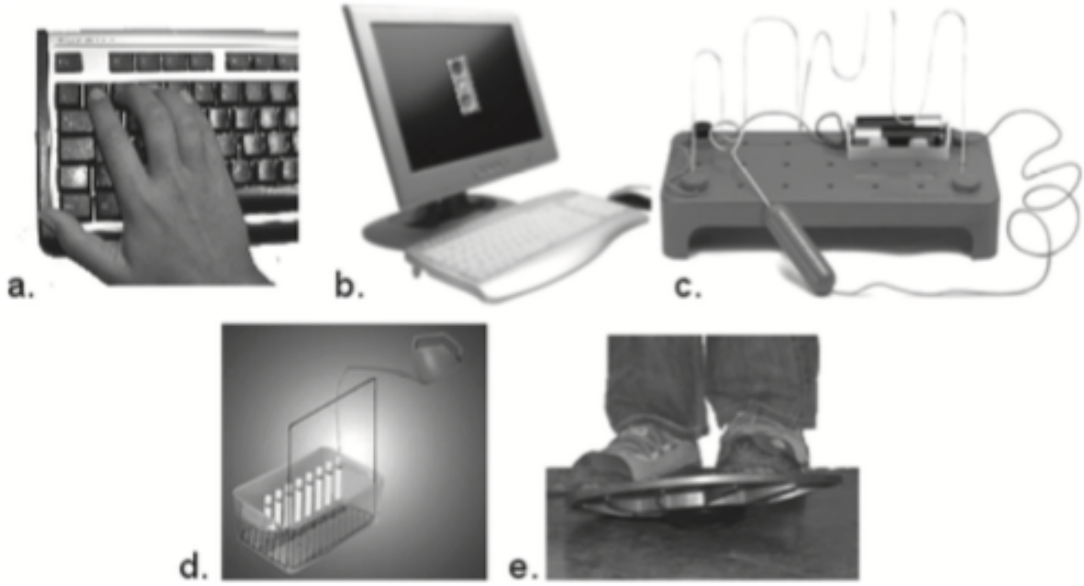

Fig. 1. Illustration of the five different tasks used to investigate: (a.) motor sequence performance; (b.) reaction time; (c.) and (d.) oculomanual performance; and (e.) body balance.

Analysis

The performance of each participant was measured at three different times: baseline performance (T0); performance after training (T1) and consolidation (T2) (see Table I).

The data were analyzed using the Statistical Package for Social Sciences version 16.0 (SPSS) software. Five 2x3 repeated measures (Analyses of Variance - ANOVAs) with factors of group type (Non-Athletes x Expert Athletes) and Time of Measurement (T0 x T1 x T2) were conducted. The Greenhouse-Geisser test was used to correct for lack of sphericity. These analyses allowed for comparisons between mean performances within and between groups, across time. The coefficient of variation (CV) was also computed at each time point per group and per task (see Table II). CV is a normalized measure of dispersion, defined as the ratio of the standard deviation to the mean (SD/mean), allowing further assessment of consistency of performance. This coefficient is frequently used given its simplicity. The CV allows comparison of relative variability of two data sets. It is mainly used to assess and compare variability of measures in biomechanics and motor control (e.g., Mullineaux, Bartlett, & Bennett, 2001, Ofori, Samson & Sosnoff, 2010), but also is used in multitask acquisition (Patterson & Carter, 2010) or a search for temporal re-organization of movement involving motor planning, execution and memory formation

(Bove, Tacchino, Pelosin, Moisello, Abbruzzese, & Ghilardi, 2009). Here, this coefficient was used to describe the dispersion in data, not in terms of kinematics, but in terms of correct performance or errors. A small CV would indicate greater consistency of performance or in error rate (across time or across groups). Here, the following intervals were used to rank dispersion: low dispersion if the CV values were less than 10%; medium dispersion if CV values were between 10% and 20%; high dispersion for CV values between 20% and 30%; and very high dispersion for CV values higher than 30% in agreement with previous research (Mullineaux, Bartlett, & Bennett, 2001).

Results

	Task	T0		T1		T2	
		Mean	SD	Mean	SD	Mean	SD
Athletes	Finger Tapping (correct sequences)	10.20	4.86	16.77	3.70	21.07	5.17
	Reaction Time (seconds)	590	88	520	71	500	86
	Circuit Trail (seconds)	29.40	6.90	22.20	6.11	22.74	5.52
	Pouring Task (seconds)	28.40	8.73	16.18	3.46	14.71	3.08
	Balance Task (errors)	15.20	4.87	6.75	4.16	7.67	3.16
Non-Athletes	Finger Tapping (correct sequences)	8.05	4.20	14.29	5.54	17.22	6.75
	Reaction Time (seconds)	640	83	550	63	530	55
	Circuit Trail (seconds)	33.76	9.27	23.75	6.11	23.57	6.08
	Pouring Task (seconds)	33.14	9.71	21.95	7.54	19.73	8.32
	Balance Task (errors)	15.90	3.33	9.43	5.72	9.52	4.32

Table I. – Descriptive statistics. Mean performance values and Standard Deviation for all tasks across different time measures, T0, T1 and T2.

		T0	T1	T2
Athletes	Finger Tapping Sequence	0,48***	0,22**	0,25**
	Reaction Time Task	0,15*	0,14*	0,17*
	Circuit Trail	0,23**	0,28**	0,24**
	Pouring Task	0,31***	0,21***	0,21***
	Balance Task	0,32***	0,62**	0,41**
Non-Athletes	Finger Tapping Sequence	0,52***	0,39***	0,39***
	Reaction Time Task	0,13*	0,11*	0,10
	Circuit Trail	0,27**	0,26**	0,26**
	Pouring Task	0,29**	0,34***	0,42***
	Balance Task	0,21**	0,61***	0,45***

Table II. - Descriptive statistics. Coefficient of Variation for all tasks across different time measures, T0, T1 and T2. * Represents Medium dispersion (CV > 10%); ** Represents High dispersion (20% < CV < 30%); *** Represents Very High Dispersion (CV > 30%).

Three different time performance measures were considered in the two groups (Athletes and Non-Athletes): T0, T1 and T2. The aim was to investigate putative differences in performance scores between the two groups, at each of these time points.

The correlation between years of practice and performance in all tasks for the expert group was also investigated. For this analysis Bivariate Pearson correlations among the three time performance measure for the five tasks and years of practice for the Athletes group were computed. No significant correlations ($p < 0.05$) were found for all but the balance task in T1 and T2, indicating that there was a decrease in error rate after acquisition and consolidation with years of practice for the expert group. For the remaining tasks (other than balance) our results indicate that independently of the years of practice (mean = 7.3 yrs, SD = 3.5) performance remains similar in the athlete group (see Table III).

T0	Pearson Correlation	,087	-,123
	Sig. (p)	,590	,445
T1	Pearson Correlation	,264	-,376*
	Sig. (p)	,096	,015
T2	Pearson Correlation	,242	-,370*
	Sig. (p)	,127	,017

Table III. - Descriptive statistics. Pearson Correlation for the Balance Task in Athletes across different time measures T0, T1 and T2. * Represents correlations that are significant at 0.05 level (2-tailed).

Task 1 - Finger Tapping Sequences (Motor Sequences)

A 2x3 repeated measures ANOVA (group vs. time) shows a significant main effect of time on task performance ($F(1.68,65.45) = 191.09$, $p = 0.001$). Bonferroni corrected tests for multiple comparisons showed significant differences between T0 and T1 ($p = 0.001$) and between T1 and T2 ($p = 0.001$). Hence, in both groups performance changed (from T0 to T1) and both groups enhance their performance by 23% in the consolidation period (from T1 to T2, given by the relative difference between T1 and T2). A significant main effect of group was also found: Athletes executed more sequences compared to Non-Athletes ($F(1,39) = 3.401$, $p = 0.036$). This was true across all time points. Athletes performed better at baseline and maintained this difference across time (see Fig.2a).

The CV analysis on performance on the motor sequence task, showed very high performance variability for both groups in T0 (48% for Athletes; 52% for Non-Athletes) and a decrease of variability in T1, leading to high variability for Athletes (23%) and very high variability for Non-Athletes (38%). This result shows that performance is less variable across time for Athletes, when compared with Non-Athletes. Variability scores were not altered from T1 to T2 in both groups.

Task 2 - Reaction Time Task (time response to visual stimuli)

A 2x3 repeated measures ANOVA (group vs time) was computed, showing a significant main effect of time ($F(1.23,47.90) = 41.95$, $p = 0.001$). Bonferroni tests corrected for multiple comparisons showed significant differences across time between T0 and T1 ($p = 0.001$) and between T1 and T2 ($p = 0.001$). These results indicate that performance increased over trials with a reduction in reaction time in both groups. Thus, both Athletes and Non-Athletes showed a significant effect of learning. Moreover, both groups benefited from the consolidation period, showing a 4% enhancement after 24 hours without additional training. A significant main effect of group was also found: Athletes had significantly smaller reaction times compared to Non-Athletes ($F(1,39) = 3.50$, $p = 0.035$). This was true across all time points. Hence, Athletes performed better at baseline (Athletes = 591msec and Non-Athletes = 645msec) and maintained this difference across time (see Fig.2b).

The CV analysis on performance in the reaction time task indicates that both groups maintain medium variability of performance across time (Athletes: 15% at T0, 14% at T1, 17% at T2; Non-Athletes: 13% at T0, 11% at T1, 10% at T2). These results indicate that both Athletes and Non-Athletes had similar consistency in performance across time.

Task 3 - Circuit Trail (Oculomanual task)

A 2x3 repeated measures ANOVA (group vs time) and report a significant main effect of time ($F(1.68,65.64) = 66.00$, $p < 0.001$). This indicates that, independently of the group in question, performance was enhanced across time. Bonferroni corrected tests for multiple comparisons showed that performance was enhanced only from T0 to T1 ($p = 0.001$), but not from T1 to T2 ($p = 0.776$). No other effects were found (see Fig.2c).

Both groups had high performance variability at all time measurements. CV was similar for both groups with a variation between 20% and 30%. (Athletes: 24% at T0, 28% at T1, 24% at T2; Novices: 28% at T0; 26% at T1, 26% at T2). This indicates that performance variability was stable between groups and within groups across time.

Task 4 - Pouring Task (Oculomanual task)

As in the other tasks, a 2x3 repeated measures ANOVA (group vs. time) was conducted, showing a significant main effect of time ($F(1.17,45.58) = 148.12$, $p = 0.001$), and a significant main effect of group ($F(1,39) = 6.303$, $p = 0.008$). Bonferroni corrected tests for multiple comparisons showed that the main effect of time was verified between T0 to T1 ($p = 0.001$) and between T1 to T2 ($p = 0.001$). In other words, performance of both groups is enhanced across time points and resulted in a 10% improvement following the consolidation period (from T1 to T2). Hence, Athletes performed better than Non-Athletes at baseline (Athletes: T0 = 28.40, SD = 8.73; Non-Athletes: T0 = 33.14, SD = 9.71). However, the relative effects of learning and consolidation were similar for both groups (see Fig.2d).

On the previous oculomanual task (Circuit Trail), both groups presented stable variability in performance across time. This was not the case for the present oculomanual task (Pouring Task). Both groups present very high CV at baseline (Athletes: 31% at T0; Non-Athletes: 30% at T0). However, with learning and consolidation, Non-Athletes and Athletes diverge. Non-Athletes showed higher variability while Athletes decreased performance variability at T1 and T2 (Athletes: 21% at T1, 21% at T2; Non-Athletes 34% at T1; 42% at T2).

Task 5 - Balance Task (Body adaptations to instability of the CG)

A 2x3 repeated measures ANOVA (group vs. time) was conducted, showing a significant main effect of time on performance ($F(1.30,50.68) = 68.05$, $p = 0.001$). Bonferroni corrected tests for multiple comparisons showed significant differences between T0 and T1 ($p = 0.001$) but not between T1 and T2 ($p = 0.233$). In other words, it seems that none of the groups benefited from the consolidation period. No other effects were found. Performance at each time point did not differ between groups (see Fig.2e).

Despite the observed performance enhancement from T0 to T1 in both groups, variability also raises from T0 to T1 (Athletes: 32% at T0, 61% at T1; Non-Athletes: 20% at T0, 60% at T1). However, this increase trend in CV reverses from T1 to T2 (Athletes: 41% at T2; Non-Athletes: 45% at T2). It seems that during the learning phase (T0 to T1) of the balance task, the consistency of proficiency was lost. However, this consistency was partially recovered with consolidation.

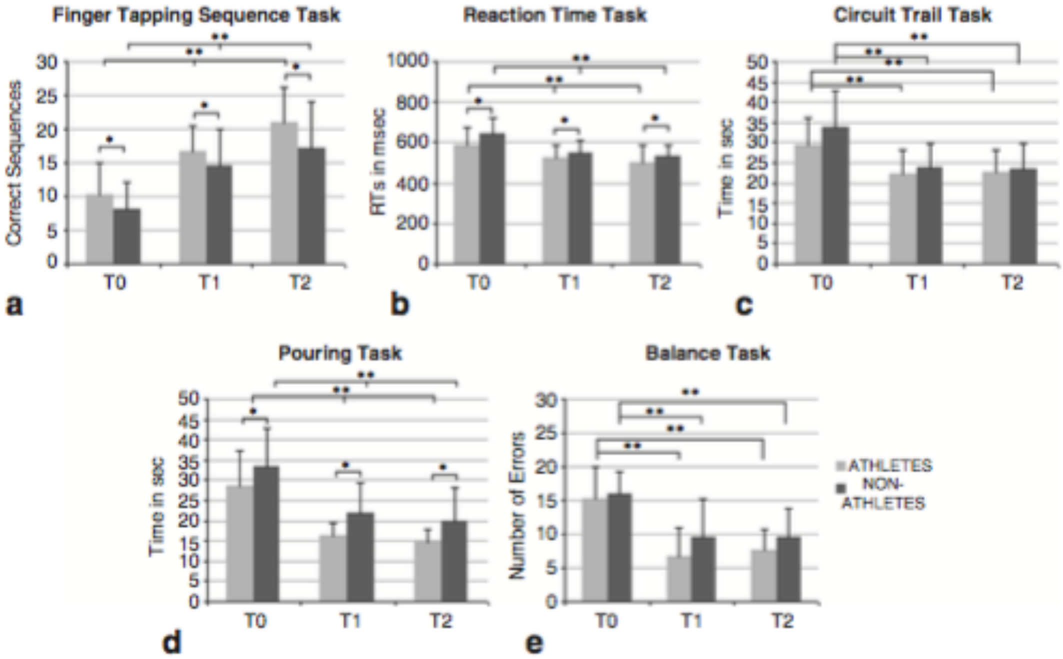

Fig. 2. Mean performance scores for all tasks: (a.) Finger Tapping Sequence task; (b.) Reaction Time task; (c.) Circuit Trail task; (d.) Pouring task; and (e.) Balance task - across different time measures (T0, T1, T2) for Athletes and Non-Athletes. Error bars represent standard deviation. Asterisks indicate significant comparisons (* for $p < 0.05$; ** for $p < 0.001$) within groups across different time measures and between groups for the same time measure.

Discussion

In this study, the effect of motor memory consolidation was investigated across different tasks (with different motor complexity requirements) in a group of Athletes (Experts) and a group of Non-Athletes. For all participants, tasks were novel.

The present results show that learning different tasks leads to different motor memory consolidation processes independently of the level of expertise (Athletes or Non-Athletes). Surprisingly, Athletes had better performance than Non-Athletes at T0 for three of the five novel tasks (Motor sequences, Reaction time, and Pouring task). Learning and consolidation led to changes in performance on both groups, as shown by the ameliorations in performance after consolidation (24 hours post-training without practice) on these tasks. Experts did not consolidate motor memories in a more efficient way (at least when one considers a 24 hour period) compared to Non-Athletes in any of these tasks. In the remaining two tasks (Circuit Trail and Balance Task) there were no differences in initial mean performance between groups, nor was there a better consolidation after initial learning practice on athletes.

The CV analysis shows similar variability values at T0 on the Finger tapping sequence and Pouring tasks. Performance variability decrease across time points T1 and T2 was larger for Athletes than for Non-Athletes in the Finger tapping task. Conversely, in the Pouring task, the decrease in performance variability for T1 and T2 by the Expert group contrasted with an increase in performance variability across time points for Non-Athletes. These unexpected findings point toward the need to rethink the single-task / single group paradigm to investigate the vicissitudes of motor memory consolidation.

According to Kelso (1982), a motor program is assumed to be an internal representation of a movement sequence. Here, Athletes did not show an expected effect, as they did not consolidate motor memories more proficiently than Non-Athletes. It is possible that this might be related with a putative high motor program specificity of gymnasts. If this is the case, and new motor memories are indeed anchored on previously consolidated motor memories, highly specific memories might not aid the formation of new memories when these are incompatible with the pre-existing ones. Additional support for this was previously described by Fourkas, Bonavolonta, Avenanti and Aglioti (2008), whom reported (using TMS and electromyography) that task specific practice of tennis players induces corticospinal facilitation during tennis imagery but not golf or table-tennis imagery. However, here, Athletes performed better at baseline than Non-Athletes on three of the five novel motor tasks. It is possible that these differences between Athletes and Non-Athletes be task-related, where performance of compatible novel motor schemes is increased in baseline as well as subsequent consolidation phases; and incompatible novel motor schemes are not aided by previously established motor memories. Thus, compatible novel motor schemes might go through an internal stimulation, the so-called "forward model", which is updated with learning (for review see Yarrow, Brown, Krakauer, 2009).

Crucially, these findings suggest differences in consolidation of new motor memories on different tasks, that are not dependent of expertise. Previous studies showed significant gains on novel task performance after a consolidation period without additional training (Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002; Baraduc, Lang, Rothwell, & Wolpert, 2004; Wu, Kansaku, & Hallet, 2004; Fischer, Nitschke, Melchert, Erdmann & Born, 2005). However these studies were based on single-task paradigms and led to general (task-unrelated) models for motor memory consolidation. Here, independently of motor expertise, both groups present a significant enhancement of performance in the consolidation period. This enhancement occurred without additional training, in only three of five novel motor tasks. Thus, according to the present study, it is not possible to generalize single task performance after consolidation like others have done up to now.
Specifically three tasks showed improved performance after consolidation (24 hours after training): 23% (Finger tapping sequence task); 4% (Reaction time task) and 10% (Pouring task). Performance in the remaining tasks (Circuit trail and Balance tasks) did not improve after the 24-hour consolidation period. Several authors (Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002; Della-Maggiore, 2005; Fischer, Nitschke, Melchert, Erdmann, & Born, 2005; Stickgold & Walker, 2005; Backhaus & Junghanns, 2006) stated that enhancement in performance after consolidation may be sleep dependent. In the current

study, sleep was controlled by instructing and confirming that all participants had a good night's sleep (≈ 8 hours).

The gains in performance over consolidation showed different CV values for Athletes and Non-Athletes. Both groups started the learning process with similar performance variability. However, Athletes showed a decrease in CV after learning and consolidation for the motor sequence and Pouring tasks. Decrease in variability can interpreted as an indication of more proficient learning and consolidation processes.

Despite the similar variabilities, and the similar learning and consolidation effects on performance (from T0 to T1 to T2) in the reaction time task in Athletes and Non-Athletes, Athletes were faster than Non-Athletes across all time points. Smaller RT's in Karate Athletes (compared to Non-Athletes), have been associated to expertise-dependent tasks where anticipatory responses are required (e.g. Mori, Ohtani, & Imanaka, 2002). However, these authors did not report differentiated RT performance for Non-Athletes and Athletes on simple RT tasks. The present results are thus very surprising, as Athletes were significantly faster than Non-Athletes on the simple reaction time task used here. It is possible that the specificity of gymnastics, requiring strength, flexibility, speed, agility, balance, reaction time and coordination, is beneficial for this type of task. Researchers should compare Athletes from different sporting backgrounds to investigate this question further.

Hadj-Bouziane, Frankowska, Meunier, Coquelin, and Boussaoud (2006) concluded that oculomanual tasks could support consolidation performance in sequential learning strategies. This finding supports the differences found between our two oculomanual tasks (Pouring and Circuit trail tasks). It is possible that the Pouring task required a sequential strategy (since one needs to fill tubes with water, one after the other, one could possibly develop a sequence with the correct timings needed to finish filling each tube and to move on to the next one), while the Circuit trail task, with its unforseen changes in vertical direction, would not benefit from such an unpredictable strategy.

On the balance task, performance was similar for both groups across time: improvement in performance after practice and stabilization of performance with consolidation. A recent review (DiStefano, Clark, & Padua, 2009) shows that elite athletes can improve static balance by training on different balance tasks. Moreover, performance on a balance task can be ameliorated along a 4-week training program (Sforza, Grassi, Turci, Fragnito, Pizzini & Ferrario, 2003). Here, it is shown that despite better performance by athletes, performance on T1 was identical to performance on T2 in each group. This suggests that consolidation of motor balance memories has no influence on expertise when considering only a 24 hour delay and possible gains might only appear later. These findings are in keeping with a temporal difference in the consolidation process or with motor memory transitions in the brain, during the consolidation process (Kassardjian, Tan, Chung, Heskin, Peterson, & Broussard, 2005; Shutoh, Ohki, Kitazawa, Itohara, & Nagao, 2006).

Park, Lee, Han, Lee, Lee, Park, & Rhyu (2009) state that the capacity of the human brain to consolidate new motor memories is dependent on plasticity phenomena. Consolidation can thus have differential effects depending on the task to be learned and the learner's previous expertise. It is thus extremely important to develop training plans that take into consideration the tasks to be learned and the specific of consolidation periods. Consequently, it seems that performance should be evaluated after the consolidation period and not immediately after training because the training gains might only be assessed at a later stage.

Athletes showed better acquisition (performance at T0 - Different starting point) of new motor schemes for certain novel motor tasks (given by task scoring). However, these differences between Athletes and Non-Athletes were not observed on all tasks. The internal models of previous motor tasks can either interfere or facilitate learning of new motor memories (Baumeister, Reinecke, Liesen, & Weiss, 2008).

Here, it is shown that, in order to understand the underlying mechanisms behind motor memory consolidation, one must use multiple-task paradigms. Different motor tasks seem to be differently consolidated as a result of the recruitment of specific consolidation models. The present findings seem to point out that consolidation relies on the complexity and constraints of the motor task to be learned. It is possible that consolidation also depends on the previously consolidated motor schemes acquired throughout sports practice. Hence, in the future, investigating learning and consolidation processes across different sports using neuroimaging techniques should also be considered. This will enable a further understanding of the effects of expertise on consolidation of novel motor memories.

No sizable differences in memory formation or consolidation were found. However, the fact that significant differences (between Athletes and Non-Athletes) were found for baseline performance (without a formed associated memory), shows a specific expert-benefit for acquisition that is not maintained throughout memory formation and consolidation. This information seems crucial for sports psychology and training. If one knows where along a timeline, differences in performance of an action derive from, (i.e. encoding, retrieval, mental comparison stages, other training biases, etc.) than, one might concentrate on training tactics that can be influenced by expertise. Such knowledge might lead to optimal coaching and learning strategies.

Although this research did not follow a theoretical or model-specific prediction, it was based on several motor memory formation and/or consolidation study designs (Fisher, Nitschke, Melchert, Erdmann, & Born, 2005; Baraduc, Lang, Rothwell, & Wolpert, 2004; Wu, Kansaku, & Hallet, 2004; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002). This somewhat diverse set of studies has produced a common finding: after learning a task, performance ameliorates without additional training. However these studies did not investigate possible differences that might occur between tasks and between different populations (such as expert Athletes and Non-Athletes). Others have investigated the components of motor memory formation revealing the existence of fast and slow components of motor memory formation (Luft & Buitrago, 2005; Lee & Schweighofer, 2009). Although these studies suggest the influence of previous motor memories in novel motor adaptations, they do not seek to clarify the direct impact or modulatory effects of previous expertise (when expertise differences are used to characterize groups).

Specifically, Lee and Schweighofer (2009) have shown that motor learning and consolidation models cannot be generalized.

Thus, this study, aimed at understanding if there are differences in motor memory acquisition, formation and consolidation across different tasks and groups, bridges this gap. Ultimately, the objective was to verify if previous experience might influence acquisition and consolidation according to the task in question (previous studies generalized single-task motor memory consolidation models to all motor schemes). The present results do not allow for a new model of motor memory formation and consolidation, but they do show that despite the absence of differences between these two phases of memory formation, acquisition can be modulated by expertise and task-specificities. These results might contribute to a better understanding of the existing models and shed new light on future studies that might further clarify these specificities and how task and previous experience might be related.

A follow-up study using different sports experts such as those not needing complex motor schemes to complete their sporting task (joggers, for example) and expert gamers who possess a set of relevant motor memories, but no need for physical training, should provide relevant information concerning what specific training backgrounds provide a better setup for the formations and consolidation of new motor memories
Here, evidence that the process of motor memory acquisition, formation and consolidation is task- and expertise-specific, was provided. Hopefully, these new insights will contribute to the development of optimal training programs for high performance athletes.

References

Abbott, R. D., White, L. R., Ross, G. W., Masaki, K. H., Curb, J. D., & Petrovitch, H. (2004) Walking and dementia in physically capable elderly men. *The Journal of the American Medical Association*, 292, 1447-1453.

Abreu, A. M., Macaluso, E., Azevedo, R., Cesari, P., Urgesi, C., & Aglioti, S. M. (2012) Action anticipation beyond the action observation network: An fMRI study in expert basketball players. *European Journal of Neuroscience,* 35, 1646-1654.

Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008) Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience,* 11, 1109-1116.

Albouy, G., Sterpenich, V., Balteau, E., Vandewalle, G., Desseilles, M., Dang-Vu, T., Darsaudi, A., Ruby, P., Luppi, P. -H., Degueldre, C., Peigneux, P., Luxen, A., & Maquet P. (2008). Both the hippocampus and striatum are involved in consolidation of motor sequence memory. *Neuron,* 58, 261-272.

Backhaus, J., & Junghanns, K. (2006) Daytime naps improve procedural motor memory. *Sleep Medicine,* 7, 508-512.

Baraduc, P., Lang, N., Rothwell, J. C., & Wolpert, D. M. (2004) Consolidation of dynamic motor learning is not disrupted by rTMS of primary motor cortex. *Current Biology,* 14, 252-256.

Baumeister, J., Reinicke, K., Liesen, H., & Weiss, M. (2008) Cortical activity of skilled performance in a complex sports related motor task. *European Journal of Applied Physiology,* 104, 625-631.

Bove, M., Tacchino, A., Pelosin, E., Moisello, C., Abbruzzese, G., & Ghilardi, M. F. (2009) Spontaneous movement tempo is influenced by observation of rhythmical actions. *Brain Research Bulletin,* 80, 112-127.

Brisswalter, J., Collardeau, M., & René, A. (2002) Effects of acute physical exercise characteristics on cognitive performance. *Sports Medicine,* 32*,* 555-566.

Cai, D. J., & Rickard, T. C. (2009) Reconsidering the role of sleep for motor memory. *Behavioral Neuroscience,* 123, 1153-1157.

Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E., & Haggard P. (2005) Action observation and acquired motor skills: An FMRI study with expert dancers. *Cerebral Cortex,* 15, 1243-1249.

Cavaco, S., Anderson, S. W., Allen, J. S., Castro-Caldas, A. & Damásio, H. (2004) The scope of procedural memory in amnesia. *Brain,* 127, 1853-1867.

Costa, R. M., Cohen, D., & Nicolelis, M. A. (2004) Differential cortical plasticity during fast and slow motor skill learning in mice. *Current Biology,* 14, 1124-1134.

Criscimagna-Hemminger, S. E. & Shadmehr, R. (2008) Consolidation patterns of human motor memory. *Journal of Neuroscience,* 28, 9610-9618.

Della-Maggiore, V. (2005) Motor memory consolidation, night and day. *The Journal of Neuroscience,* 25, 9067-9068.

Dishman, R. K., Berthoud, H. R., Booth, F. W., Cotman, C. W., Edgerton, V. R., Fleshner, M. R., Gandevia, S. C., Gomez-Pinilla, F., Greenwood, B. N., Hillman, C. H., Kramer, A. F., Levin, B. E., Moran, T. H., Russo-Neustadt, A. A., Salamone, J. D., Van Hoomissen, J. D., Wade, C. E., York, D. A., & Zigmond M. J. (2006) Neurobiology of Exercise. *Obesity,* 14, 345-356.

DiStefano, L. J., Clark, M. A., & Padua, D. A. (2009) Evidence supporting balance training in healthy individuals: a systemic review. *Journal of Strength and Conditioning Research,* 23, 2718-2731.

Eggermont, L., Swaab, D., Luiten, P., & Scherder, E. (2005) Exercise, cognition and Alzheimer´s disease: More is not necessarily better. *Neuroscience and Biobehavioral Reviews*, 30, 562-575.

Ferris, L. T., Williams, J. S. & Shen, C. L. (2007) The effect of acute exercise on serum brain-derived neurotrophic factor levels and cognitive function. *Medicine Science Sport Exercise*, 39, 728–734.

Filippi M., Ceccarelli, A., Pagani, E., Gatti, R., Rossi, A., Stefanelli, L., Falini, A., Comi, G., & Rocca, M. A. (2010) Motor learning in healthy humans is associated to gray matter changes: A tensor-based morphometry study. *PLoS One,* 5, e10198.

Fischer, S., Nitschke, M. F., Melchert, U. H., Erdmann, C. & Born, J. (2005) Motor memory consolidation in sleep shapes more effective neuronal representations. *The Journal of Neuroscience,* 25, 11248-11255.

Fourkas, A. D., Bonavolonta, V., Avenanti, A., & Aglioti, S. M. (2008) Kinesthetic imagery and tool-specific modulation of corticospinal representations in expert tennis players. *Cerebral Cortex*, 18, 2382-290.

Hadj-Bouziane, F., Frankowska, H., Meunier, M., Coquelin, P., & Boussaoud, D. (2006) Conditional visuo-motor learning and dimension reduction. *Cognition Process,* 7, 95-104.

Hutchinson, S., Lee, L. H., Gaab, N., & Schlaug, G. (2003) Cerebellar volume of musicians. *Cerebral Cortex,* 13, 943-949.

Hyde, K. L., Lerch, J., Norton, A., Forgeard, M., Winner, E., Evans, A. C., & Schlaug, G. (2009) Musical training shapes structural brain development. *The Journal of Neuroscience,* 29, 3019-3025.

Kassardjian, C. D., Tan, Y., Chung, J. J., Heskin, R., Peterson, M. J., & Broussard, D. M. (2005) The site of a motor memory shifts with consolidation. *The Journal of Neuroscience*, 25, 7979-7985.

Kelso, J. A. S. (1982) *Human Motor Behavior*. New Jersey: Lawrence Erlbaum Associates, Inc.

Krakauer, J. W. (2009) Motor learning and consolidation: the case of visuomotor rotation. *Advances in Experimental Medicine and Biology,* 629, 405-421.

Krakauer, J. W., & Shadmehr, R. (2006) Consolidation of motor memory. *Trends in Neuroscience,* 29, 58-64.

Kuriyama, K., Stickgold, R., & Walker, M. P. (2004) Sleep-dependent learning and motor-skill complexity. *Learning and Memory,* 11, 705-713.

Lalazar, H. & Vaadia, E. (2008) Neural basis of sensorimotor learning: modifying internal models. *Current Opinion in Neurobiology,* 18, 573-581.

Larson, E. B., Wang, L., Bowen, J. D., McCormick, W. C., Teri, L., Crane, P., Kukull, W. (2006) Exercise is associated with reduced risk for incident dementia among persons 65 years of age and older. *Annals of Internal Medicine,* 144, 73-81.

Lee, J., & Schweighofer, N. (2009) Dual adaptation supports a parallel architecture of motor memory. *The Journal of Neuroscience,* 29, 10396 –10404.

Luft, A. R., & Buitrago, M. M. (2005) Stages of motor skill learning. *Molecular Neurobiology,* 32, 206-216.

Mori, S., Ohtani, Y., & Imanaka, K. (2002) Reaction times and anticipatory skills in karate athletes. *Human Movement Science,* 21, 213-230.

Mullineaux, D. R., Bartlett, R. M., & Bennett, S. (2001) Research design and statistic in biomechanics and motor control. *Journal of Sports Sciences*, 19, 739-760.

Ofori, E., Samson, J. M., & Sosnoff, J. J. (2010) Age-related differences in force variability and visual display. *Experimental Brain Research,* 203, 299-306.

Olson, I. R., Rao, H., Moore, K. S., Wang, J., Detre, J. A., & Aguirre, G. K. (2006) Using perfusion fMRI to measure continuous changes in neural activity with learning. *Brain and Cognition,* 60, 262-271.

Ostry, D. J., Darainy, M., Mattar, A. A., Wong, J., & Gribble, P. L. (2010) Somatosensory plasticity and motor learning. *Journal of Neuroscience,* 30, 5384-5393.

Park, I. S., Lee, K. J., Han, J. W., Lee, N. J., Lee, W. T., Park, K. A., & Rhyu, I. J. (2009) Experience-dependent plasticity of cerebellar vermis in basketball players. *Cerebellum,* 8, 334-339.

Patterson, J. T., & Carter, M. (2010) Learner regulated knowledge of results during the acquisition of multiple timing goals. *Human Movement Science,* 29, 214-227.

Rickard, T. C., Cai, D. J., Rieth, C. A., Jones, J., & Ard, M. C. (2008) Sleep does not enhance motor sequence learning. *Journal of Experimental Psychology: Learning, Memory and Cognition,* 34, 834-842.

Russmann, H., Lamy, J., Shamim, E., Meunier, S., & Hallett, M. (2009) Associative plasticity in intracortical inhibitory circuits in human motor cortex. *Clinical Neurophysiology,* 120, 1204–1212.

Scherder, E. J., Van Paasschen, J., Deijen, J. B., Knokke, V. D., Orlebeke, J. F., Burgers, I., Devriese, P. -P., Swaab, D. F., Sergeant, J. A. (2005) Physical activity and executive functions in the elderly with mild cognitive impairment. *Aging & Mental Health,* 9, 272-280.

Sforza, C., Grassi, G. P., Turci, M., Fragnito, N., Pizzini G., & Ferrario, V. F. (2003) Influence of training on maintenance of equilibrium on a tilting platform. *Perceptual Motor Skills,* 96, 127-136.

Shutoh, F., Ohki, M., Kitazawa, H., Itohara, S., & Nagao, S. (2006) Memory trace of motor learning shifts transsynaptically from cerebelar cortex to nuclei for consolidation. *Neuroscience,* 139, 7667-777.

Smyth, C., Summers, J. J., & Garry, M. I. (2010) Differences in motor learning success are associated with differences in M1 excitability. *Human Movement Science.* 29, 618-630.

Starr, J. M., Leaper, S. A., Murray, A. D., Lemmon, H. A., Staff, R. T., Deary, R. T., & Whalley, L. J. (2009) Brain white matter lesions detected by magnetic resonance imaging are associated with balance and gait speed. *Journal of Neurology Neurosurgery and Psychiatry,* 74, 94-98.

Stickgold, R., & Walker, M. (2005) Memory consolidation and reconsolidation: What is the role of sleep? *Trends in Neurosciences,* 28, 408-415.

Tervaniemi, M. (2009) Musicians-same or different? *Annals of the New York Academy of Sciences,* 1169, 151–156.

Tomassini, V., Jbabdi, S., Kincses, Z. T., Bosnell, R., Douaud, G., Pozzilli, C., Matthews, P. M., & Johansen-Berg, H. (2010) Structural and functional bases for individual differences in motor learning. *Human Brain Mapping,* 32, 494-502.

Vertes, R. P. (2004) Memory Consolidation in Sleep: Dream or Reality. *Neuron*, 44, 135-148.

Walker, M. P., Brakefield, T., Morgan, A., Hobson, J. A., & Stickgold, R. (2002) Practice with sleep makes perfect: Sleep dependent motor skill learning. *Neuron,* 35, 205-211.

Walker, M. P., Brakefield, T. J., Hobson, A., & Stickgold, R. (2003) Dissociable stages of human memory consolidation and reconsolidation. *Nature,* 425, 616-620.

Walker, M. P., & Stickgold, R. (2005) Memory consolidation and reconsolidation: What is the role of sleep? *Trends in Neuroscience,* 28, 408-415.

Watson, A. H. (2006) What can studying musicians tell us about motor control of the hand? *Journal of Anatomy,* 208, 527-542.

Wei, G., & Luo, J. (2010) Sport expert's motor imagery: Functional imaging of professional motor skills and simple motor skills. *Brain Research,* 1341, 51-62.

Williams, A. M., Ward, P., Knowles, J. M. & Smeeton, N. J. (2002) Anticipation skill in a real-world task: Measurement, training and transfer in tennis. *Journal of Experimental Psychology. Applied,* 8, 259-270.

Winter, B., Breitenstein, C., Mooren, F. C., Voelker, K., Fobker, M., Lechtermann, A., Krueger, K., Fromme, A., Korsukewitz, C., Floel, A., Knecht S. (2007) High impact running improves learning. *Neurobiology of Learning and Memory,* 87, 597-609.

Wu, T., Kansaku, K. & Hallet, M. (2004) How self-initiated memorized movements become automatic: A functional MRI study. *Journal of Neurophysiology,* 91, 1690-1698.

Yarrow, K., Brown, P., Krakauer, J. (2009) Inside the brain of an elite athlete: the neural processes that support high achievement in sports. *Nature Reviews Neuroscience,* 10, 585-596.

SECOND STUDY

Pereira, T., Castro-Caldas, A., & Abreu, A. M. (2014). Age-related Gender Differences in Motor and Inhibitory Learning and Consolidation. Journal of Advanced Neuroscience Research, 1, 10-21.

Journal of Advanced Neuroscience Research

Age-related Gender Differences in Motor and Inhibitory Learning and Consolidation

Pereira, T.[1,2], Castro-Caldas, A.[2] & Abreu, A. M.[3,*]

1. Institute of Health Sciences, Portuguese Catholic University, Lisbon, Portugal
2. Laboratory of Physical Activity and Health, *Instituto Superior Dom Afonso III*, Loulé, Portugal
3. *Universidade Europeia*, Laureate International Universities, Lisbon, Portugal

*. Corresponding Author

Abstract

Aim: The understanding of the neural correlates of motor learning and consolidation has seen significant progress in recent years. Such advances have afforded the development of better training plans and the potentiation of motor skill learning in sports, in neurological recovery or simply in everyday life. However, the variations in motor learning and consolidation across different ages are still not well understood. In order to investigate this, we assessed performance in two different tasks (Finger Tapping Sequence and Go/No-Go tasks) in four different Age-groups (Children; Young Adults; Mature Adults, and Seniors).

Materials and Methods: The two tasks were executed across three different time periods (T0, T1 and T2), during which performance was measured: Day 1. Baseline (T0) and Performance After Training – i.e. Learning (T1) and; Day 2. Consolidation Performance – 24 hours post-T1 without any additional training (T2).

Results: We show that the group of Seniors did not enhance performance 24 hours post-training in the Finger Tapping Sequence task, while all the other Age-groups did. There were no differences in performance in Children, but age and sex interacted to enhance performance. This complex mechanism was shown to be task-specific. Moreover, none of the Age-groups enhanced performance in T2 in the Go/No-Go Task, but we found a Female advantage after practice in Mature Adults and Seniors.

Conclusions: The influence of both age and sex in task performance and consolidation is to be taken into consideration in order to ameliorate training and potentiate individual capacities while delaying age-related impairments.

Introduction

Learning a new set of motor skills as well as relearning previously acquired ones is fundamental not only for everyday life activities but also constitutes an extremely important means to improve rehabilitation programs following brain injuries that affect motor performance [1]. Amelioration in motor performance can be achieved via online gains reported during training sessions and also by means of offline gains without additional training [2]. These offline gains can be modulated by the structure of practice [3], and are of paramount importance, as they represent additional motor performance gains after the end of a training session without additional training. In a previous study with young adults, we showed that different motor tasks could have different off-line gains [4]. Here, we aim to investigate how these off-line gains are modulated across the lifespan.

A considerable amount of research has been dedicated to the psychophysical consequences of aging, focusing on how to avoid impairments in motor learning and re-learning, essential for our daily activities, and on the mechanisms and procedures that allow the potentiation of motor and cognitive memory acquisition and recall across different ages [e.g., 5-7]. It has been well established that cognitive-motor activities facilitate neuro-protection [8]. However, the specific importance of motor activity and mental exercise for the brain across different age groups is still unclear. Specifically, we know that there can be an increase in the brain's white matter by training working memory in older adults [9]. However, these findings report to training in cognitive tasks. But what consequences are expected when training occurs in motor tasks? Such a query was addressed in a study where older adults are shown to be able to shift between implicit and explicit learning when a new motor sequence is being learned [10]. Despite this ability to alternate between learning types, most studies have focused more on degeneration and impairment in brain functions with age, and less on learning capabilities [e.g., 11-15]. Accordingly, most studies have investigated physical exercise and motor behavior as ways to enhance, otherwise deteriorated performance in older subjects [e.g., 16, 17]. One such example relates to the benefits brought by physical exercise that can be mediated by the enhancement of Brain-Derived Neurotrophic Factor - BDNF [18] that can positively interfere with some neurodegenerative diseases such as Alzheimers' Disease [19]. Moreover, physical activity has been shown to enhance time response in older and in middle-aged people, and ameliorate the planning/execution of a response as well as the executive functions mediated by the prefrontal cortex [20]. Learning and consolidating a motor sequence task seems to activate cortical and sub-cortical structures such as the basal ganglia, cerebellum, suplementary motor, primary motor and premotor areas [21-24]. Furthermore, some authors found the hippocampus to be implicated not just on the learning phases, but also in the consolidation phases of a motor memory [25, 26]. It is possible that some neurodegenerative diseases that typically occur in older ages, in which the functioning of the hippocampus is compromised [e.g., 27], might consequently affect the process of motor memory consolidation. Two other structures involved on the initial phase of motor sequence learning are the frontal cortex and the striatum. Accordingly, task-dependent deficits may be attributed to the age-associated degeneration in cortico-striatal networks [28, 29]. However, recent neuroimaging studies shed new light on the aging brains' function and it seems that a better way to describe connectivity in the brain's networks in the mature brain, is not by means of describing its deficits, but by understanding its changes in functionality that may decline, maintain or even improve [30]. Specifically, age-related changes in connectivity are consistent with increased emotion regulation and decreased cognitive functions [31]. Moreover, preservation of cognitive functions in older adults has been associated to compensatory mechanisms associated to neuroanatomical and functional changes leading to an overall increase in, albeit less efficient, functional connectivity [32]. Crucially, and in what pertains to our study, aging may alter the connectivity of brain networks underlying motor learning by increasing the bilateral-frontal and fronto-parietal connectivity [33].

Although it has been well established that motor performance tends to decline in older ages [34], and that healthy older subjects experience significant declines in motor skill acquisition when compared to younger subjects [35], it remains unclear how off-line enhancements are modulated with motor memory consolidation across age. As such, contrasting data arise from a study by Smith and collaborators [36] showing an age resistant component of motor memories, compared to declines in motor learning and performance with age. Very little data is available to add on to this discussion, Dorfberger and collaborators [37] have shown no differences when learning or retaining new motor memories, between children and adolescents. However, children were less susceptible to interference when compared to adolescents: i.e., newer motor memory experiences affect the consolidation process of previously learned motor memories in young adults, but not in children. Nevertheless, these authors did not compare these younger groups with adults or seniors. According to these and the aforementioned data, there are several brain and behavioral changes that occur across the lifespan that might compromise the ability to learn and consolidate new motor memories. This can have a tremendous impact in the aging persons' everyday life, as lifelong motor learning should help increase and maintain motoric independence.

It thus seems paramount to investigate motor performance and consolidation across the lifespan. Specifically, the capacity to learn and consolidate a novel motor sequence or to simply perform an action and/or to inhibit that same action on cue, are important requisites in everyday life activities. Here we will investigate these exact capabilities. Finally, it is important to note that previous research has already demonstrated the existence of sex differences in motor task learning, but not performance, given by a male advantage, enhanced during adolescence compared to younger groups [38]. However, and to the best of our knowledge, the analysis of sex differences throughout the lifespan, from infancy to old age, has not been described and is mostly ignored due to the structure of the protocols. Here, we attempt to discriminate the influence of gender in age-related motor learning and consolidation and we discuss our results in light of the latest neuroscientific available data pertaining to functional and architectural changes across the lifespan.

Methods

Participants

One hundred and twenty eight neurotypical subjects (64 male and 64 female) participated in this study and were divided into four age groups: 32 (16 female) Children (aged 8-9 years old; M = 8.75; SD = 0.44 years); 32 (16 female) Young Adults (aged 20-25 years old; M = 21.88; SD = 1.57 years); 32 (16 female) Mature Adults (aged 40-45 years old; M = 42.58; SD = 1.98 years) and 32 (16 female) Seniors (aged 65-70 years old; M = 67.29; SD = 2.05 years). Participants were recruited from Primary Schools, Universities, Local workplaces and Nursing homes (from the Algarve area, Portugal), respectively. All participants were right handed and had no outstanding medical condition that might impair fine motor performance.

Procedures

Participants and the participants' parents or guardians (in the case of minors) gave their written informed consent prior to participating in the experimental tasks and received information concerning the experimental procedures. This study was conducted in accordance with the tenets of the Declaration of Helsinki (2008). The participants' performance was assessed in two different tasks (Finger Tapping Sequence and Go/No-Go Tasks) in order to investigate motor learning, and consolidation across different age groups. The assessment was conducted in accordance with the procedures previously described by Pereira and collaborators [4] Each task was first performed in a Training Session (T0 to T1). During this session, Baseline Performance – T0 (first time the subject executed the task) and Performance after training – T1 (average of the last 3 trials) – were assessed. Subsequently, all subjects were re-tested on the same tasks, after a 24-hour delay without additional training (Consolidation Session –T2). The 24-hour period without additional training, allowed for consolidation, as described in previous designs [e.g., 39]. Each participant was randomly assigned to start out with either the Finger Tapping Sequence or the Go/No-Go Task. Participants were tested in a silent and dimly lit room with the fewest distractors possible. Participants were instructed to have a good night of sleep (7 to 9 hours) between T1 and T2 (24 hour-period). All subjects met this inclusion criterion.

Apparatus

Both tasks were presented on a computer screen and participants were seated at a distance of ± 60 cm from the computer screen. For the Finger Tapping Sequence, participants were instructed to tap a 5 number sequence on the computer keyboard (task described bellow). The Go/No-Go task, on the other hand, was developed using Super Lab 4.5 and was also presented on a computer screen. Here, the aim was to either respond motorically or inhibit the motor response to the stimuli presented on the computer screen as described bellow. In both tasks, the participants were instructed to tap the sequence, press a button or inhibit the motor response as quickly and accurately as possible.

Tasks

Finger Tapping Sequence

As reported in previous studies [e.g., 40, 41], learning a novel motor task, such as the Finger Tapping Sequence task, should progress through a series of unique memory stages. Specifically, performance should initially improve during training and continue to improve even without additional training after a 24-hour period. Here we intended to verify how such performance might be modulated across different Age-groups and sexes.

The participants were required to learn a Finger Tapping Sequence (4_1_3_2_4) by using a computer keyboard. The finger sequence corresponded to computer keys as follows: digit 1 – Index finger; digit 2 – Middle finger; digit 3 – Ring finger; digit 4 – Little finger (see Figure1). The participants were requested to repeat the sequence as quickly and as accurately as possible for 30 seconds. Each 30-second trial was initiated and terminated by an auditory signal cue. The participants were instructed to tap the movement sequence continuously until hearing the stop signal, and to continue without pause, even if committing any error, as quickly and accurately as possible. Performance was given by the number of correctly typed sequences. The training session consisted of twelve 30-second trials with 30-second rest periods in between trials lasting ± 12 min in total [42]. Baseline Performance (T0) consisted on the first 30-second trial, whereas Performance After Training (T1) was given by the mean of the last 3 trials. The Consolidation Session (T2) consisted of three 30-second trials with 30-second rest periods between trials, executed 24 hours post-T1, without additional training. T2 performance consisted on the mean of all three 30-second trials executed during the consolidation session. All sequences were recorded on the computer throughout the completion of the trials.

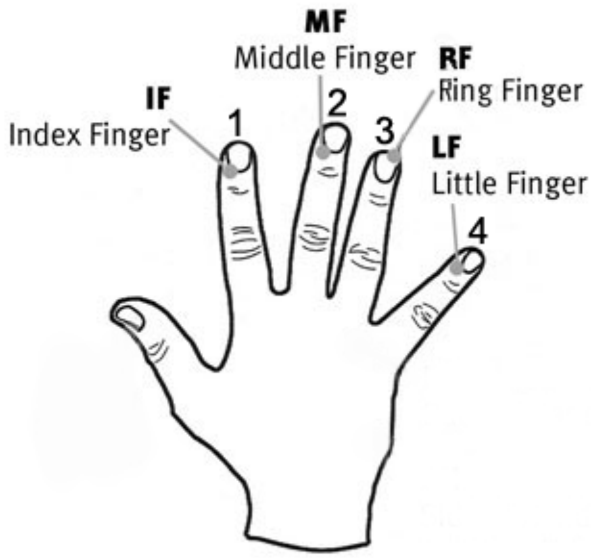

Figure 1. Digit-to-finger correspondence for the Finger Tapping Sequence task (Sequence: 4_1_3_2_4).

Go/No-Go Task

Understanding the control of motor inhibition is extremely important, as it constitutes a significant part of everyday life. Inhibitory control is an executive function, i.e. a higher cognitive function involved in the executive control of behavior that has been linked to motor coordination [43]. Certain fast inhibitory actions are not processed at a conscious level and are in close relation with the response reaction time to a certain stimulus. Hence, a better understanding of inhibitory performance might help in developing new motor learning strategies. In order to tap this issue, we assessed performance in a Go/No-Go task across different Age-groups and sexes.

The participants were requested to answer to arrow stimuli presented on a computer screen as fast and as accurately as possible. The stimuli consisted of four arrows (right or left green and right or left red) that were randomly presented (60 arrow presentations in total per block). Each arrow stimulus remained onscreen for 1000 ms, after which the participant could no longer answer. The participants were instructed to press the right mouse button as a response to a green arrow to the right, to press left mouse button as a response to a green arrow to the left and to refrain from pressing any button when any of the red arrows (left or right) were presented (see Figure 2). The participants were also instructed to answer as quickly and accurately as possible. When a mouse button was pressed the fixation cross would immediately appear. If no answer would take place, the fixation cross would appear 1000 ms later. Either way, a fixation cross trial would always intersperse the arrow trials. The experiment included twelve 60-trial blocks (1 trial = 1 arrow) with 30 sec rest periods between blocks, lasting ± 30 min in total. This procedure was used to maintain a similar protocol and rest periods as the Finger Tapping Sequence. The arrows were randomly presented and were 50% green and 50% red, in order to avoid motor learning. Although, in the Finger Tapping Sequence Task, performance was only given by accuracy, here, performance was measured by means of two dependent variables: a) Speed – given by the reaction time to respond to the green arrows (measure of speed) and; b) Accuracy – given by 1 - the number of errors made (measure of accuracy). Errors were computed when one either pressed the right button when a left arrow was presented, or pressed the left button in view of a right arrow, or simply pressed any button in the presence of a red arrow. Both accuracy and speed were recorded *via* the SuperLab software used to develop the stimuli.

In order to integrate both speed and accuracy in one overall index of performance [e.g. 44, 45], we computed the Inverse Efficiency Score (IES) by dividing, for each Time condition (T0, T1, & T2) and in each subject, the mean correct reaction time by the percentage of correct responses. The IES was introduced by Townsend and Ashby [46] to control for speed–accuracy trade-off effects (i.e. when movement speed increases, movement accuracy decreases [47], as it combines accuracy and reaction times in a single measure. Worse overall performance is given by higher scores.

In conformance with the Finger Tapping Sequence task, we assessed IES at T0 that consisted on the ratio between the mean RT and the proportion of correct responses obtained during the first block constituted by 60 trials; IES_T1, on the other hand, consisted on the ratio between the mean RT and the proportion of correct responses obtained during the three last 60-trial blocks of the training session; Finally, IES_T2 consisted on the ratio between the mean RT and the proportion of correct responses obtained from the average of the three 60-trial blocks executed 24 hours after training.

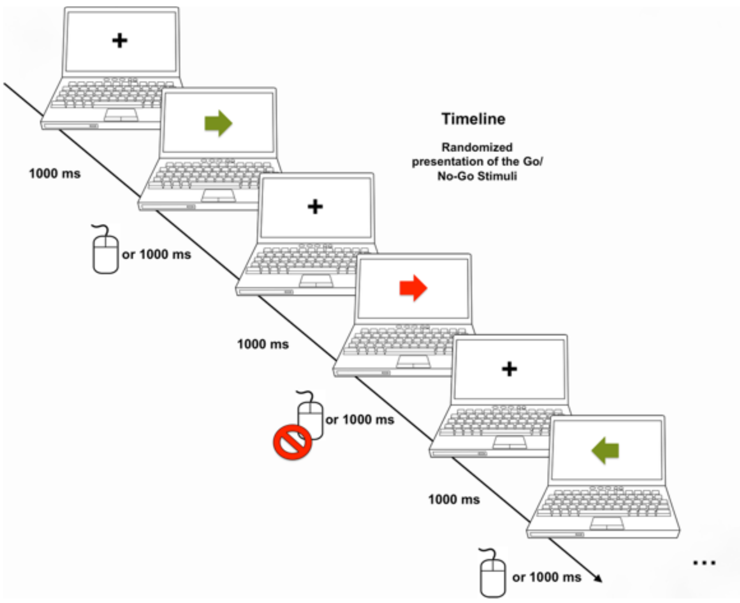

Figure 2. Go/No-Go task. Stimuli timeline. Each of the four arrows (red left and right and green left and right) was presented randomly for 1000 milliseconds interspersed with fixation crosses. Participants were instructed to press the right mouse button in response to the right green arrow; the left mouse button in response to the left green arrow and to refrain from pressing any button in the presence of any of the two red arrows.

Results

In order to investigate motor learning and consolidation performance, we considered performance measurements across three different time periods for the two tasks, in the four age groups. Here, we aimed to investigate performance given by accuracy in the Finger Tapping Sequence task, and by accuracy and speed integration (i.e. the speed accuracy tradeoff) in the Go/No-Go task across the different time periods (Learning and Consolidation) and across age groups.

The data were entered into separate 4 x 2 x 3 Mixed Repeated Measures Factorial ANOVAs (Group x Sex x Time), with group type (Children x Young Adults x Mature Adults x Seniors) and Sex (Male x Female) as between-subjects covariates and time of measurement as within-subjects factors (T0 x T1 x T2), for each task. Bonferroni corrected Post hoc multiple comparisons were performed.

Finger Tapping Sequence Task

Concerning the Finger Tapping Sequence Task, we computed a Repeated Measures ANOVA, as stated above, and found a significant main effect of Time ($F(2,240) = 492.170$, $p = 0.001$). Bonferroni adjusted pairwise comparisons indicate that there were performance gains from T0 ($M = 4.133$; $SE = 0.203$) to T1 ($M = 8.070$; $SE = 0.201$) to T2 ($M = 10.039$; $SE = 0.252$) (all $p = 0.001$). Globally, the participants enhanced their performance from baseline assessment, to assessment after training to the 24 hours post-training assessment (i.e. off-line gains that enhance motor performance without additional training after a 24 hour interval). We also found a significant main effect of Age-Group ($F(3,120) = 194.126$, $p = 0.001$). Bonferroni adjusted pairwise comparisons indicate that Young Adults ($M = 13.563$; $SE = 0.378$) outperform Mature Adults ($M = 7.781$; $SE = 0.378$), whom in turn, outperform Children ($M = 5.417$; $SE = 0.378$), all of which outperform Seniors ($M = 2.896$; $SE = 0.378$) (all $p = 0.001$). On the other hand, we did not find a significant main effect of Sex ($F(1,120) = 1.502$, $p = 0.223$), which is to say that gender *per se* did not modulate performance in the Finger Tapping Sequence task.

We did, however, find two-way interaction effects between Time and Age-Group ($F(6,240) = 37.204$, $p = 0.001$) and between Time and Sex ($F(2,240) = 22.179$, $p = 0.001$). Finally, we report a three-way interaction effect between Time, Age-Group and Sex ($F(3,120) = 2.707$, $p = 0.015$). Bonferroni adjusted pairwise comparisons show that the off-line enhancement of performance (Consolidation), without additional training, did not occur in Mature Adult Males ($p > 0.05$) and in Female Seniors ($p > 0.05$). Moreover, not only did Male Seniors not benefit from 24-hour post-training off-line gains, they also did not benefit from training in the first place (i.e. in the Male Senior group, T0 does not differ from T1 or T2 and T1 and T2 do not differ between them, all $p > 0.05$). All other comparisons were highly significant, showing across-group gains from T0 to T1 to T2 (all $p = 0.001$). Furthermore, Bonferroni adjusted multiple comparisons show differences between Sex groups, according to Time and Age-Groups. In T0, only Young Male (M = 10.875; SE = 0.511) and Young Female Adults (M = 5.375; SE = 0.511) differ in their performance ($p = 0.001$), as Males outperform Females; In T1, both Young Male (M = 15.563; SE = 0.535) and Young Female Adults (M = 13.125; SE = 0.535) ($p = 0.002$), and Male (M = 2.438; SE = 0.535) and Female Seniors (M = 4.563; SE = 0.535) ($p = 0.006$) differ in their performance. However, while Young Male Adults outperform Females, we find the opposite pattern in Seniors, with Females outperforming Males; Finally, in T2, only Children present similar performances between sexes ($p > 0.05$), while Young Male (M = 20.375; SE = 0.624) and Young Female Adults (M = 16.063; SE = 0.624) ($p = 0.01$), Mature Male (M = 9.125; SE = 0.624) and Mature Female Adults (M = 11.563; SE = 0.624) ($p = 0.01$), and Male (M = 2.438; SE = 0.624) and Female Seniors (M = 4.938; SE = 0.624) ($p = 0.01$), show differences in performance, with Males outperforming Females as Young Adults and losing this advantage as Mature Adults and Seniors (see Figure 3).

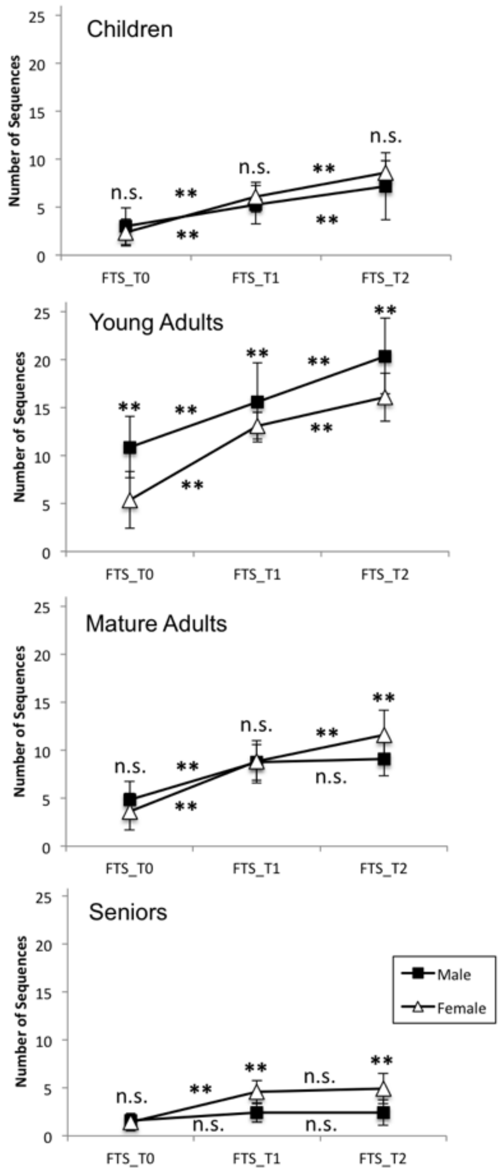

Figure 3. Across-session performance gains for males and females of the four age groups in the Finger Tapping Sequence task. Performance accounts for mean number of correct sequences. FTS_T0 consists on the mean number of sequences in the first 30-sec trial; FTS_T1 consists on the mean number of sequences in the last three trials of the training session; FTS_T2 consists on the mean number of sequences in the three 30-sec trial executed 24 hours after training. Bars represent standard deviation of the mean. ** indicate significant comparisons ($p < 0.01$).

Go/No-Go Task

The IESs were entered into a Repeated Measures ANOVA using the same procedure as in the Finger Tapping Sequence Task analysis. As with the previous task, we found a significant main effect of Time ($F(2,240) = 33.159$, $p = 0.001$). Bonferroni adjusted pairwise comparisons indicate that there were performance gains from T0 (M = 926.822; SE = 27.151) to T1 (M = 786.142; SE = 16.155) to T2 (M = 742.726; SE = 16.488) (all $p < 0.05$, higher scores indicate worse performances). As before, the participants enhanced their performance from baseline assessment, to assessment after training to the 24 hours post-training assessment. Although subtle, the off-line gains without additional training after a 24 hour-interval, were significant. Once again, we found a significant main effect of Age-Group ($F(3,120) = 123.297$, $p = 0.001$). Bonferroni adjusted pairwise comparisons indicate that Young Adults (M =457.098; SE = 30.798) outperform Mature Adults (M = 812.085; SE = 30.798) and the Children's group (M = 726.440; SE = 30.798) (both $p = 0.001$), although Mature Adults and Children do not present any differences in performance ($p = 0.309$), all groups outperform Seniors (M = 1278.632; SE = 30.798) (all $P = 0.001$). In striking contrast with the Finger Tapping Sequence task, the Go/No-Go does present a significant main effect of Sex ($F(1,120) = 29.025$, $p = 0.001$), which is to say that gender *per se* does modulate performance in the Go/No-Go task, whereby Females (M = 735.601; SE = 21.778) outperform Males (M = 901.526; SE = 21.778), $p = 0.001$.

Again, we found an interaction effect found between Time and Sex ($F(2,240) = 7.686$, $p = 0.001$), however, no interaction effect between Time and Age-Group was found ($F(6,240) = 2.017$, $p = 0.064$), this is to say that performance across time is not differently modulated by the different Age Groups. Finally, we report a three-way interaction effect between Time, Age-Group and Sex ($F(6,240) = 6.371$, $p = 0.001$). Bonferroni adjusted pairwise comparisons show that the off-line enhancement of performance (Consolidation), without additional training, did not occur in any of the age groups ($p > 0.05$) and improvement from T0 to T1 in overall IES occurred only in Children ($p = 0.002$) and Seniors ($p = 0.002$). However, when considering the sexes separately, we find that differences between T0 and T1 are supported only by Male Children ($p = 0.020$). Moreover, we uncover a significant enhancement in Mature Female Adults, from T0 to T1 ($p = 0.024$) and verify that the amelioration in performance, from T0 to T1, in Seniors was also due to the Female participants ($p = 0.001$). So it seems that training benefits Male Children and Mature and Senior Female participants, while off-line gains without training, i.e., consolidation, does not occur in any Sex or Age-group. Importantly, across time, Children's performance (M = 855.184; SE = 54.301) equals that of Mature Adults (M = 872.447; SE = 54.301) in T0; ($p = 1.000$), but is worse than that of Young Adults (M = 525.383; SE = 54.301) and better than that of Seniors (M = 1454.274; SE =54.301); (both $p = 0.001$). After Training, in T1, on the other hand, differences in performance between Children (M = 684.822; SE = 32.311) and Mature Adults (M = 810.594; SE = 32.311) arise, as Children outperform Mature Adults ($p = 0.041$). Finally, in T2, these differences are lost as Children (M = 639.313; SE = 32.975) and Mature Adults (M = 753.214; SE = 32.311), both show similar performances ($p = 0.096$). Conversely, all other Age-Groups perform differently across time-points as discussed above (see Figure 4).

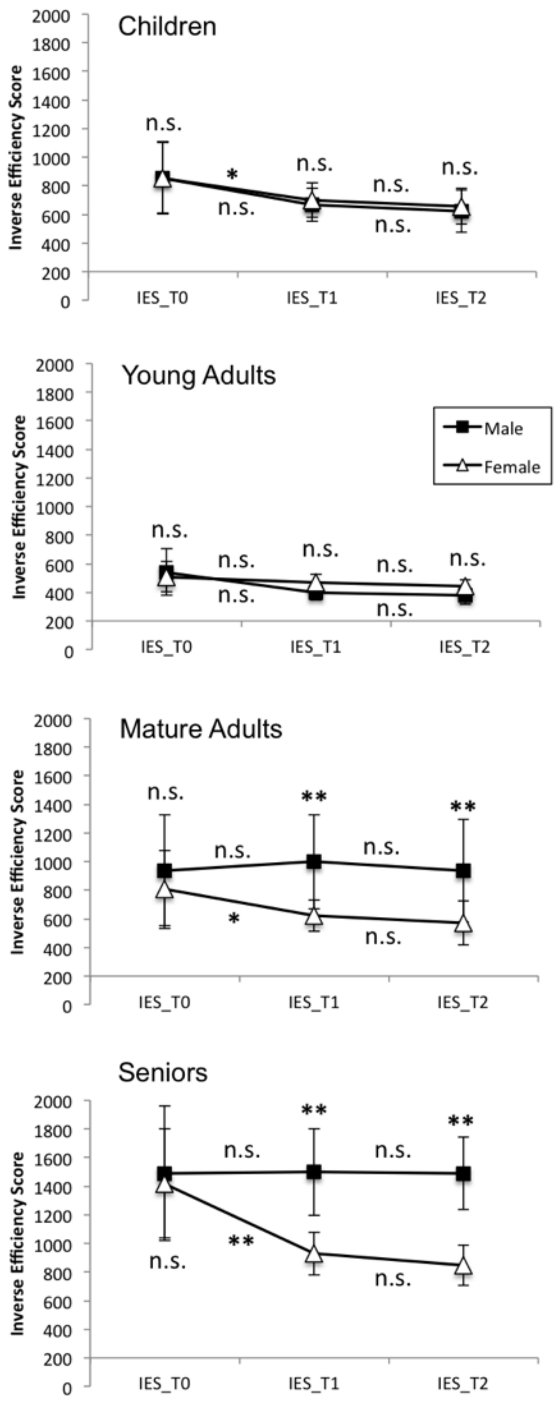

Figure 4. Across-session performance gains for males and females of the four age groups in the Go/No-Go task. Performance for IES_T0 consists on the ratio between the mean RT and the proportion of correct responses obtained during the first block constituted by 60 trials; IES_T1 consists on the ratio between the mean RT and the proportion of correct responses obtained during the three last 60-trial blocks of the training session; IES_T2 consists on the ratio between the mean RT and the proportion of correct responses obtained from the average of the three 60-trial blocks executed 24 hours after training. Bars represent standard deviation of the mean. * Indicates significant comparisons ($p < 0.05$) ** indicate significant comparisons ($p < 0.01$).

Discussion

One of our main findings points to a lack of Consolidation effect in Seniors in both tasks. As in previous investigations, older adults are the only group where no positive effects of consolidation can be imprinted on performance. These results are in accordance with previous studies where older adults do not show consolidation benefits in motor sequence tasks [48-50]. Although our results show the existence of offline gains in three of the four age groups (Children, Young Adults and Mature Adults), these gains are only associated to the finger Tapping Sequence Task. It is possible that the neural requirements involved in motor memory establishment (implicated in the consolidation of the Finger Tapping Sequence task), might not translate equally in a task that predominantly involves online decision-making (as required by the Go/No-Go task). This is particularly curious given that Verbruggen and Logan [51] have shown that stimulus-stop associations can indeed be trained in Go/No-Go tasks. It thus seems that when it comes to Consolidation, both task and/or Age-Group might have an effect. These differences can be associated with the age degeneration that occurs in cortico-striatal networks [28, 29] that might be differently implicated in motor memory and inhibition control tasks. This is consistent with previous studies showing that different executive functions result from the interplay of different cortical systems [52]. Concurrently, overall performance can be differently modulated by sexes according to Age-group, as shown predominantly in Young and Mature Adults and Seniors, but not in Children. Previous studies had already shown that motor performance generally improves from childhood to young adulthood and from there, decreases well into old age [53]. Other studies have consistently shown a growing male advantage in motor performance from childhood to adolescence [e.g., 38]. However, and to the best of our knowledge, none have investigated the complex interactions between sexes and age (from childhood to old age), as we have tapped here. According to previous studies [40, 41] there is a great effect of Consolidation on performance that leads to enhancements of around 20 to 30% in motor sequence performance. Our results reveal that this performance enhancement without additional training only occurs from childhood to adulthood, but that this effect is lost in older age. This result is in conformance with that of Wilson and collaborators [50] who found that this capacity to enhance performance during the consolidation period is lost in older age, for this specific task. Previous research has already demonstrated that the brain suffers huge plasticity phenomena each time a new memory is learned [for review see 54]. However, this plasticity is further subject to changes with aging, as certain brain areas seem to be more vulnerable to the aging process [for review see 55].

The hippocampus is one of the brain structures that changes its functionality, decreasing its efficiency with age [27]. Considering the hippocampus to be an important structure that, together with the striatum is implicated in the consolidation process [25, 56], it might be possible to re-adapt the training and rehabilitation plans in Seniors, by means of alternative tasks requiring mostly different brain structures in order to optimize their performance gains.

In agreement with Dorfberger and collaborators [57], we also found sequence specific post-training gains in performance in Children performing a motor sequence (Finger Tapping Sequence task). Their data did not reveal any specific differences between Children (9 and 12 year olds) and Adolescents (17 year olds). Our results share the same trend also in older Age Groups – Young and Mature Adults. Here, however, we show that Seniors lose this post-training advantage. Crucially, we also show that initial (T0) and post-training performances (T1 and T2) are superior in Young adults and regress again in the older Age-groups. Importantly a Male advantage arises across testing points in the Young Adults. This Male advantage is lost in Mature Adults, whereby the only advantage occurs in Females in T2 - the offline post training gains. The Female advantage in performance is maintained in T2 in Seniors and also reappears in T1 at this Age-Group. As it seems, age and sex seem to concur to bias the complex motor processing and motor memory formation mechanisms. The development of such biases is not present in Childhood, but soon appears in Young Adults and inverts its direction as the Adults Mature. It seems, however, that this sinuous development is task-specific. Specifically, in the Go/No-Go task, differences in performance between sexes arise only in Mature Adults and are maintained stable in Seniors, whereby Females outperform Males in both T1 and T2.

Previous studies have shown that motor performance is influenced by age and sex differences from early childhood [58]. It has been well established that these early gender differences are task specific [59]. Although we did not find such differences so early on, as they are possibly more tenuous in early motor skill development, we did find these consolidated differences in the Finger Tapping Sequence task in Young adults.

Moreno-Briseño and collaborators [60] have recently suggested that different learning mechanisms, like strategic calibration and spatial alignment, may contribute differently according to gender. This might explain different sex biases according to task. But how can we explain different biases alternating with age in the same task? Other studies have shown that skill proficiency in childhood is predictive of future skill proficiency [61]. However, and according to our own results, the matter seems quite more complex. A possible explanation might stem from Weiermann and Meier's [62] recent work, whereby they show that different learning processes are implicated in learning a specific sequence, depending on age. In particular, the authors show that performance of Children and older Adults highly depends on the existence of explicit knowledge, i.e., the presence of the training sequence. However, Young Adults (aged 20 to 30 years) do not reduce performance, independently of the presence of such explicit cues. It is possible that the activation of different neural networks, associated to the different processing strategies be involved across Age-groups [e.g., 29, 63]. Specifically, explicit knowledge learning-dependent performance might be attributed to a lower striatal function that is sometimes compensated by the activation of other areas like the frontal cortex [62].

As stated before, age-related changes in connectivity and preservation of cognitive functions in older adults has been associated to compensatory mechanisms associated to neuroanatomical and functional changes that lead to an overall increase and less efficient, functional connectivity [32]. Our results aging may alter the connectivity of brain networks underlying motor learning by increasing the bilateral-frontal and fronto-parietal connectivity [33]. Thus, it is possible that the changes in connectivity compromise the enhancement without additional training that is expected during the consolidation period and observed at younger ages. Accordingly, age can be a limiting factor in terms of performance gains without additional training. Despite the group's lower performance, the Senior group was, notwithstanding, able to learn a new motor sequence. Further research is needed, however, in order to fully understand the neural correlates and differences across different age groups and how these differences might be reduced in older people.

Despite the simplicity of the Go/No-Go task, a decision making task tapping executive functions (in particular inhibition response) there were no statistically significant improvements in performance, 24 hours post-training in any of the Age-groups. Overnight sleep has been identified as essential for the activation of areas that are implicated in faster and more precise mapping of key-presses [64], however, we did not find such improvement in performance driven by motor-memory plasticity. It seems clear that the processes implicated in motor memory formation are distinct from those implicated in response inhibition. Verbruggen and Logan [51], for example, have suggested that learning a stimulus-stop association through training would create an inhibitory tag that would be retrieved in future phases. Our results do not counter this suggestion, as performance in T2 was no different from performance in T1 in any of the groups. Indeed, in a study with preschool children, Thorell and collaborators [65] have shown that despite improvements in working memory with training, no such improvements were observed in inhibition. The authors go on to suggest that this might be due to the psychological and neural processes underpinning these distinct executive functions.

Although there were no differences in Consolidation, we did find sex differences in performance after practice (T1), given by better performances of Mature Adult and Senior Females. An animal study investigating learning and inhibition [66] has shown that despite the absence of significant differences in baseline activity, Males and Females differ in their ability to form conditioned associations and inhibit responses after practice trials. It is possible that the same applies to humans. Moreover, it has been suggested that gender differences in inhibitory control, might be related to the different inhibitory demands pressing on each gender during evolution [67]. This thesis has been recently supported by Hosseini-Kamkar and Morton [68], whom put forth an evolutionary perspective to explain a Female advantage in inhibitory control. However, the authors suggest that a less impulsive behavior in females is not a trait, but a strategy employed during potentially reproductive periods. This is quite surprising, as we did not observe a Female advantage in the Go/No-Go task in Young Adults, but in Mature Adults and Seniors instead. This incongruence might be explained by a recent study by Thakkar and collaborators [69] whom did not find any sex differences in accuracy or response inhibition in a stop-signal task, but women did show greater sensitivity to trial history (flexible adjustments in speed–accuracy trade-offs and greater cognitive flexibility associated with response control). This could account for the improvement in performance in T1 (after practice trials) given by Females. It is possible that no such difference between Female and Male participants was found in Young Adults as they might have already been performing at ceiling level in T0.

As it seems, Age, Sex and Task all influence performance that is differently modulated as a result of these interacting factors. More research is needed in order to understand the distinct neural underpinnings of men and women and how it might be possible to potentiate the individual gender capacity to learn and consolidate new motor memories, while delaying age-dependent impairments by potentiating neural plasticity.

References

[1] Mang CS, Campbell KL, Ross CJ, Boyd LA. Promoting neuroplasticity for motor rehabilitation after stroke: Considering the effects of aerobic exercise and genetic variation on brain-derived neurotrophic factor. Phys Ther. 2013; 93: 1707-1716.

[2] Robertson EM, Pascual-Leone A, Miall RC. Current concepts in procedural consolidation. Nat Rev Neurosci. 2004; 5: 576–582.

[3] Kantak SS, Sullivan KJ, Fisher BE, Knowlton BJ, Winstein CJ. Neural substrates of motor memory consolidation depend on practice structure. Nat Neurosci. 2010; 13: 923–925.

[4] Pereira T, Abreu AM, Castro-Caldas A. Understanding task and expertise-specific motor acquisition and motor memory formation and consolidation. Percept Mot Skills. 2013; 117: 108–129.

[5] Ofen N, Shing YL. From perception to memory: Changes in memory systems across the lifespan. Neurosci Biobehav Rev. 2013; 37: 2258-2267.

[6] Cai L, Chan JS, Yan JH, Peng K. Brain plasticity and motor practice in cognitive aging. Front Aging Neurosci. 2014; 6: 31.

[7] Rebok GW, Ball K, Guey LT, Jones RN, Kim HY, King JW, et al. Ten-year effects of the advanced cognitive training for independent and vital elderly cognitive training trial on cognition and everyday functioning in older adults. J Am Geriatr Soc. 2014; 62: 16-24.

[8] Taubert M, Draganski B, Anwander A, Muller K, Horstmann A, Villringer A, et al. Dynamic properties of human brain structure: Learning-related changes in cortical areas and associated fiber connections. J Neurosci. 2010; 30: 11670-11677.

[9] Engvig A, Fjell AM, Westlye LT, Moberget T, Sundseth Ø, Larsen VA, et al. Memory training impacts short-term changes in aging white matter: A longitudinal diffusion tensor imaging study. Hum Brain Mapp. 2012; 33: 2390–2406.

[10] Nemeth D, Janacsek K, Fiser J. Age-dependent and coordinated shift in performance between implicit and explicit skill learning. Front Comput Neurosci. 2013; 7:147.

[11] Volkow ND, Logan J, Fowler JS, Wang GJ, Gur RC, Wong C, et al. Association between age-related decline in brain dopamine activity and impairment in frontal and cingulate metabolism. Am J Psychiatry. 2000; 157: 75-80.

[12] Sowell ER, Peterson BS, Thompson PM, Welcome SE, Henkenius AL, Toga AW. Mapping cortical change across the human life span. Nat Neurosci. 2003; 6: 309-315.

[13] Salat DH, Buckner RL, Snyder AZ, Greve DN, Desikan RS, Busa E, et al. Thinning of the cerebral cortex in aging. Cereb Cortex. 2004; 14: 721-730.

[14] Fotenos AF, Snyder AZ, Girton LE, Morris JC, Buckner RL. Normative estimates of cross-sectional and longitudinal brain volume decline in aging and AD. Neurology. 2005; 64: 1032-1039.

[15] Sullivan EV, Pfefferbaum A. Diffusion tensor imaging and aging. Neurosci Biobehav Rev. 2006; 30: 749-761.

[16] Rolland Y, Abellan van Kan G, Vellas B. Healthy brain aging: Role of exercise and physical activity. Clin Geriatr Med. 2010; 26: 75-87.

[17] Voss MW, Prakash RS, Erickson KI, Basak C, Chaddock L, Kim JS, et al. Plasticity of brain networks in a randomized intervention trial of exercise training in older adults. Front Aging Neurosci. 2010; 2: 32.

[18] Voss MW, Erickson KI, Prakash RS, Chaddock L, Kim JS, Alves H, et al. Neurobiological markers of exercise-related brain plasticity in older adults. Brain Behav Immun. 2013; 28: 90–99.

[19] Erickson KI, Weinstein AM, Lopez OL. Physical activity, brain plasticity, and Alzheimer's disease. Arch Med Res. 2012; 43: 615–621.

[20] Berchicci M, Lucci G, Di Russo F. Benefits of physical exercise on the aging brain: The role of the prefrontal cortex. J Gerontol A Biol Sci Med Sci. 2013; 68: 1337–1341.

[21] Galea JM, Vazquez A, Pasricha N, de Xivry JJ, Celnik P. Dissociating the roles of the cerebellum and motor cortex during adaptive learning: The motor cortex retains what the cerebellum learns. Cereb Cortex. 2011; 21: 1761–1770.

[22] Orban P, Peigneux P, Lungu O, Albouy G, Breton E, Laberenne F, et al. The multifaceted nature of the relationship between performance and brain activity in motor sequence learning. Neuroimage, 2010; 49: 694–702.

[23] Steele CJ, Penhune VB. Specific increases within global decreases: A functional magnetic resonance imaging investigation of five days of motor sequence learning. J Neurosci. 2010; 30: 8332-8341.

[24] Landi SM, Baguear F, Della-Maggiore V. One week of motor adaptation induces structural changes in primary motor cortex that predict long-term memory one year later. J Neurosci. 2011; 31: 11808–11813.

[25] Albouy G, Sterpenich V, Balteau E, Vandewalle G, Desseilles M, Dang-Vu T, et al. Both the hippocampus and striatum are involved in consolidation of motor sequence memory. Neuron. 2008; 58: 261–272.

[26] Gheysen F, Van Opstal F, Roggeman C, Van Waelvelde H, Fias W. Hippocampal contribution to early and later stages of implicit motor sequence learning. Exp Brain Res. 2010; 202: 795–807.

[27] Miller DB, O'Callaghan JP. Effects of aging and stress on hippocampal structure and function. Metabolism. 2003; 52: 17-21.

[28] Rieckmann A, Bäckman L. Implicit learning in aging: Extant patterns and new directions. Neuropsychol Rev. 2009; 19: 490–503.

[29] Rieckmann A, Fischer H, Bäckman L. Activation in striatum and medial temporal lobe during sequence learning in younger and older adults: Relations to performance. Neuroimage. 2010; 50: 1303–1312.

[30] Robertson Z. Lifelong learning and the aging brain. In: Bell SC, editor. Senior law handbook. Colorado: Continuing Legal Education in Colorado, Inc; 2014. p. 405-411.

[31] Hampson M, Tokoglu F, Shen X, Scheinost D, Papademetris X, Constable RT. Intrinsic brain connectivity related to age in young and middle aged adults. PLoS One. 2012; 7: e44067.

[32] Meunier D, Stamatakis EA, Tyler LK. Age-related functional reorganization, structural changes, and preserved cognition. Neurobiol Aging. 2014; 35: 42-54.

[33] Lin CH, Chiang MC, Wu AD, Iacoboni M, Udompholkul P, Yazdanshenas O, et al. Enhanced motor learning in older adults is accompanied by increased bilateral frontal and frontoparietal connectivity. Brain Connect. 2012; 2: 56–68.

[34] Degardin A, Devos D, Cassim F, Bourriez JL, Defebvre L, Derambure P, et al. Deficit of sensorimotor integration in normal aging. Neurosci Lett. 2011; 498: 208-212.

[35] Zimerman M, Nitsch M, Giraux P, Gerloff C, Cohen LG, Hummel FC. Neuroenhancement of the aging brain: Restoring skill acquisition in old subjects. Ann Neurol. 2012; 73: 10–15.

[36] Smith CD, Walton A, Loveland AD, Umberger GH, Kryscio RJ, Gash DM. Memories that last in old age: motor skill learning and memory preservation. Neurobiol Aging. 2005; 26: 883-90.

[37] Dorfberger S, Adi-Japha E, Karni A. Reduced susceptibility to interference in the consolidation of motor memory before adolescence. PLoS One. 2007; 2: e240.

[38] Dorfberger S, Adi-Japha E, Karni A. Sex differences in motor performance and motor learning in children and adolescents: An increasing male advantage in motor learning and consolidation phase gains. Behav Brain Res. 2009; 198: 165-171.

[39] Krakauer JW, Shadmehr R. Consolidation of motor memory. Trends Neurosci. 2006; 29: 58-64.

[40] Walker MP, Brakefield T, Morgan A, Hobson JA, Stickgold R. Practice with sleep makes perfect: Sleep dependent motor skill learning. Neuron. 2002; 35: 205-211.

[41] Walker MP, Brakefield T, Hobson JA, Stickgold R. Dissociable stages of human memory consolidation and reconsolidation. Nature. 2003; 425: 616-620.

[42] Kuriyama K, Stickgold R, Walker MP. Sleep-dependent learning and motor-skill complexity. Learn Mem. 2004; 11: 705-713.

[43] Michel E. Motor coordination and executive functions. Dev Med Child Neurol. 2012; 54: 971.

[44] Bruyer R, Brysbaert M. Combining speed and accuracy in cognitive psychology: Is the inverse efficiency score (IES) a better dependent variable than the mean reaction time (RT) and the percentage of errors (PE)? Psychol Belg. 2011; 51: 5-13.

[45] Rach S, Diederich A, Colonius H. On quantifying multisensory interaction effects in reaction time and detection rate. Psychol Res. 2010; 75: 77–94.

[46] Townsend JT, Ashby FG. Stochastic modeling of elementary psychological processes. Cambridge: Cambridge University Press; 1983.

[47] Fitts PM. The information capacity of the human motor system in controlling the amplitude of movement. J Exp Psychol Gen. 1992; 121: 262-269.

[48] Nemeth D, Janacsek K. The dynamics of implicit skill consolidation in young and elderly adults. J Gerontol B Psychol Sci Soc Sci. 2011; 66: 15–22.

[49] Fogel SM, Albouy G, Vien C, King BR, Hoge RD, Jbabdi S, et al. Age-related differences in cerebral activation for motor sequence learning are correlated with sleep spindles. J. Sleep Res. 2012; 21: 5.

[50] Wilson JK, Baran B, Pace-Schott EF, Ivry RB, Spencer RMC. Sleep modulates word-pair learning but not motor sequence learning in healthy older adults. Neurobio Aging. 2012; 33: 991–1000.

[51] Verbruggen F, Logan GD. Automatic and controlled response inhibition: Associative learning in the go/no-go and stop-signal paradigms. J Exp Psychol Gen. 2008; 137: 649-672.

[52] Garavan H, Ross TJ, Murphy K, Roche RAP, Stein, EA. Dissociable executive functions in the dynamic control of behavior: inhibition, error detection, and correction. Neuroimage. 2002; 17:1820–1829.

[53] Leversen JSR, Haga M, Sigmundsson H. From children to adults: Motor performance across the life-span. PLoS One. 2012; 7: e38830.

[54] Dayan E, Cohen LG. Neuroplasticity subserving motor skill learning. Neuron. 2011; 72: 443–454.

[55] Burke SN, Barnes CA. Neural plasticity in the ageing brain. Nat Rev Neurosci. 2006; 7: 30-40.

[56] Albouy G, Sterpenich V, Vandewalle G, Darsaud A, Gais S, Rauchs G, et al. Interaction between hippocampal and striatal memory systems predicts subsequent motor sequence memory consolidation. PLoS One. 2013; 8: e59490.

[57] Dorfberger S, Adi-Japha E, Karni A. Sequence specific motor performance gains after memory consolidation in children and adolescents. PloS One. 2012; 7:e28673.

[58] Toriola AL, Igbokwe NU. Age and sex differences in motor performance of pre-school Nigerian children. J Sports Sci. 1986; 4: 219-227.

[59] Raudsepp L, Paasuke M. Gender differences in fundamental movement patterns, motor performances, and strength measurements of prepubertal children. Pediatr Exerc Sci. 1995; 7: 294-304.

[60] Moreno-Briseño P, Díaz R, Campos-Romo A, Fernandez-Ruiz J. Sex-related differences in motor learning and performance. Behav Brain Funct. 2010; 6: 74.

[61] Barnett LM, van Beurden E, Morgan PJ, Brooks LO, Beard JR. Gender differences in motor skill proficiency from childhood to adolescence. Res Q Exerc Sport. 2010; 81: 162-170.

[62] Weiermann B, Meier B. Incidental sequence learning across the lifespan. Cognition. 2012; 123: 380–391.

[63] Dennis NA, Cabeza R. Age-related dedifferentiation of learning systems: An fMRI study of implicit and explicit learning. Neurobiol Aging. 2011; 32: 2318.e17.

[64] Walker MP, Stickgold R, Alsop D, Gaab N, Schlaug G. Sleep-dependent motor memory plasticity in the human brain. Neuroscience. 2005; 133: 911-917.

[65] Thorell LB, Lindqvist S, Bergman NS, Bohlin G, Klingberg T. Training and transfer effects of executive functions in preschool children. Dev Sci. 2009; 12: 106-113.

[66] Bucci DJ, Hopkins ME, Keene CS, Sharma M, Orr LE. Sex differences in learning and inhibition in spontaneously hypertensive rats. Behav Brain Res. 2008; 187: 27-32.

[67] Yuan J, He Y, Qinglin Z, Chen A, Li H. Gender differences in behavioral inhibitory control: ERP evidence from a two-choice oddball task. Psychophysiology. 2008; 45: 986-993.

[68] Hosseini-Kamkar N, Morton JB. Sex differences in self-regulation: An evolutionary perspective. Front Neurosci. 2014; 8:233.

[69] Thakkar KN, Congdon E, Poldrack, RA, Sabb FW, London ED, Cannon TD, et al. Women are more sensitive than men to prior trial events on the Stop-signal task. Br J Psychol. 2014; 105: 254–272.

THIRD STUDY

Pereira, T., Castro-Caldas, A., & Abreu, A. M. (under revision on Scientific Reports). Why Sleep when you can Run: Physical Exercise Accelerates the Consolidation of a Motor Sequence

under revision on Scientific Reports

Why Sleep when you can Run: Physical Exercise Accelerates the Consolidation of a Motor Sequence

Pereira, T.[1*], Castro-Caldas, A.[1] & Abreu, A. M.[2]

1. Institute of Health Sciences, Portuguese Catholic University, Lisbon, Portugal
2. Universidade Europeia, Laureate International Universities, Lisbon, Portugal

*. Corresponding Author

Abstract

Physical activity has a positive impact on learning and cognition. Most motor skill training happens in tandem with physical exercise. Here we aim to investigate the effects of acute physical exercise on the consolidation of a motor sequence task. Seventy two subjects were divided into three groups based on exercise intensity (REST; LOW and HIGH). All groups learned a finger tapping sequence during a training session. LOW and HIGH groups performed an acute physical exercise after the training session while the REST group remained seated. All groups were re-tested to assess motor consolidation, 1 hour, 24 hours and 7 days after the training session. Our results indicate that REST and LOW groups enhanced their performance without additional training only 24 hours after the training session. However, the HIGH group enhanced its performance without additional training 1 hour after the training session and maintain these results 24 hours and 7 days after training. These findings indicate that a bout of high intensity acute exercise can accelerate the performance enhancement without additional training previously reported several hours after the learning session.

Introduction

It is well understood that physical activity has a positive impact on brain activity and cognition[1]. However, when training a motor skill specifically associated with a certain physical activity or sports, it is important to understand the changes in the consolidation process to maximize the effects of motor learning and performance. This information is very useful either in athletes or in individuals recovering from a motor disability. It is known that the consolidation period (defined as a set of processes whereby a long-term memory becomes more stable with the passage of time[2]) for a motor sequence can span from 6-hours up to 72-hour periods[3]. This consolidation period that occurs after practice, the so-called off-line learning period, leads to significant enhancements in motor performance and is extremely important to consider, since the best performance does not occur at the end of a training session, but a few hours or even a few days after that[4].

The first reports of this off-line period enhancement on motor learning were made by Walker and collaborators[5] and were attributed to the effects of sleep and subsequent reorganization on motor memory consolidation. However, a few years since, research has shown that there is more than just sleep in this performance amelioration process[6,7,8]. Moreover, with these new insights, there is more information available that affords the investigation of different paths for motor learning and consolidation, in order to understand the effect of other factors like age[4] or task[9] than just the sleep in the consolidation of a motor task.

More than ever, society is now recognizing the benefits of physical activity, that were once, only associated to athletes, on some of the world's major diseases[10]. The latest advances in sports neuroscience have systematically shown that physical activity can prevent metabolic disturbances[11] and enhance mood and some cognitive functions[12]. It is also known that a single session of aerobic exercise can promote excitability and early plasticity in the motor cortex, not only in the regions subtending the activation of the motor effectors involved in exercise, but also in the adjacent ones[13]. Such motor cortex excitability with a single exercise session was recently supported by Gutmann and Collaborators[14] in a study investigating EEG Alpha Peak frequency in two exercise protocols. The authors found a significant increase in cortical activity after intense exercise, but not after a steady state exercise. These effects of physical activity on brain function and structure are well documented[15,13], and some research reported specific positive effects on the brain structure and function, such as enhanced plasticity that occurs on the hippocampus[16], increased brain blood volume[17], and a significant increase in Brain Derived Neurotrophic Factor (BDNF) after only a single session of aerobic exercise in young adults[18]. Furthermore, and according to this research, some of the biochemical changes that occur in the brain, like the production of BDNF, can be potentiated by progressive resistance training. However, it is still unclear how these changes can specifically affect the consolidation of a motor sequence.

Despite the fact that global and specific effects of physical activity on brain functions are well documented[13,15,19,20], one must also consider that different intensities of physical exercise might promote different effects on the muscles and energy systems, by optimizing the way we convert glucose, with the use of oxygen into energy[21]. These effects are based on different exercise intensities and result from different training programs and goals. Every time we exercise, we experience higher brain activity and body metabolism that can be proportional to exercise intensity[22]. Based on the findings described above we investigated the influence of a single bout of exercise on the consolidation of a motor sequence learning task. This will shed new light on how the consolidation process of a motor sequence reacts to acute exercise and will complement the influence of other factors like sleep, age or tasks as described above, understanding how physical exercise can be used to enhance training and recovery plans.

Results

We computed a repeated measures ANOVA 3 x 5 (Group x Time), with group Exercise types (REST, LOW and HIGH) and performance assessment times (T0, T1, T2, T3 and T4). Our goal was to investigate the effects of exercise (with low and high intensity) on the consolidation of a motor sequence. Bonferroni corrected Post hoc multiple comparisons were also performed.

We found a significant main effect of Time ($F(8,276) = 27.441$, $p = 0.001$) and Bonferroni adjusted pairwise comparisons indicate that there were performance gains across time in all three groups (REST, LOW and HIGH Exercise), but only the HIGH Exercise group registered significant differences 1 hour after training (from T1 to T2) (Mean Difference = -3.917; SE = 0.593 $p = 0.001$), maintaining this performance 24 hours after training (from T2 to T3) (Mean Difference = 0.83; SE = 0.514 $p = 1.000$) and 7 days after training (from T3 to T4) (Mean Difference = 1.417; SE = 0.535 $p = 0.143$).

The REST group maintained motor performance from T1 to T2 (measured 1 hour after training) (Mean Difference = 0.167; SE = 0.143 $p = 1.000$). Also, the LOW Exercise group had the same performance from T1 to T2 (measured 1 hour after training) showing no additional performance gains after the physical exercise (Mean Difference = 0.667; SE = 0.299 $p = 0.358$), thus differentiating from the HIGH Exercise group.

Our results showed that the expected enhancement on performance without additional training, that happened 24 hours after the training session according to literature and our previous research (Pereira et al., 2013; Pereira et al., 2014) appeared in the HIGH Exercise group, 1 hour after the training of the motor sequence as described above. However, such an enhancement only appeared in the remaining two groups (REST and LOW) 24 hours after training (from T1 to T3) as showed by the Bonferroni adjusted pairwise comparisons for the REST Group (Mean Difference = -2.417; SE = 0.158 $p = 0.001$) and LOW Exercise Group (Mean Difference = -2.917; SE = 0.158, $p = 0.001$). All groups maintain their performance when we comparing the 24-hour with the 7-day post-training measurements, showing no additional improvements in motor sequence performance after a 7-day period without additional training (Mean Difference = 0.444; SE = 0.219 $p = 0.460$). This could indicate that the consolidation of the sequence was established 24 hours after the training session , for the REST and LOW groups and 1 hour after the Training Session for the HIGH group and that it remains stable for at least one week independently on the type of exercise.

Globally, the participants enhanced their performance from baseline (T0), to performance after training (T1), and registered an enhancement without additional training, 24 hours after training and maintain these performance gains up to 7 days after the training session. However when it comes to the performance 1h after the training, only the HIGH intensity exercise group was able to enhance their performance and anticipate the positive effects of consolidation on a motor sequence. The HIGH intensity exercise group enhance it's performance without additional training 1 hour after the training session while the other two groups (REST and LOW Exercise), only enhance the performance without additional training 24 hours after the training session.

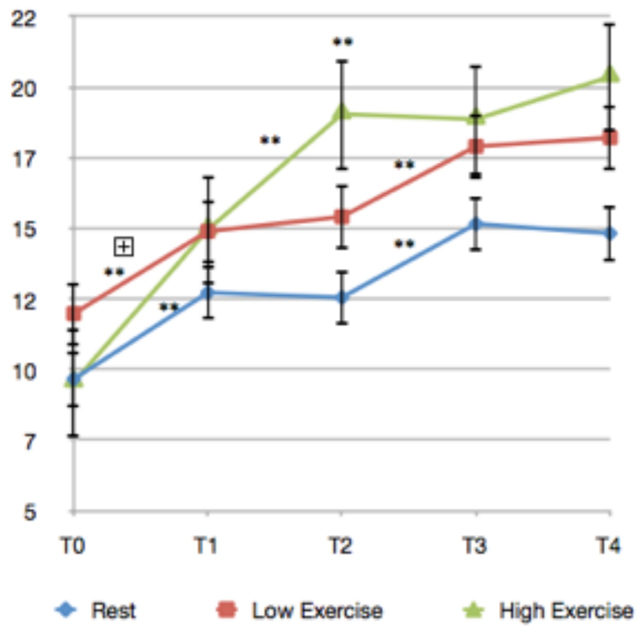

Figure 1. Performance of the Finger Tapping Sequence on the 3 groups (Rest, Low Intensity and High Intensity Exercise). Across-session performance gains for the three groups in the Finger Tapping Sequence task. Performance accounts for mean number of correct sequences. T0 consists on the mean number of sequences in the first 30-sec trial; T1 consists on the mean number of sequences in the last three trials of the training session; T2 consists on the mean number of sequences in the three30-sec trial executed 1 hour after training. T3 consists on the mean number of sequences in the three 30-sec trial executed 24 hours after training T4 consists on the mean number of sequences in the three 30-sec trial executed 7 days after training. Bars represent standard error of the mean. indicate significant comparisons ($p < 0.001$).

Discussion

Our study addressed three main issues. The first, concerned the influence of a single bout of exercise on the consolidation of a motor sequence task; the second, concerned the putative differences between two exercise intensities on the performance of that motor sequence; and finally, the third, concerned the optimal period, associated to physical exercise, needed for consolidation.

Our results are in agreement with several studies that found a positive effect of acute physical activity on different brain functions, like visual attention[23], motor inhibition[24] and also in motor memory[25] like our investigation. However, these studies used different protocols and goals, that do not allow a clear comparison or a clarification of what is the best exercise protocol or strategy to potentiate the effects of exercise. Furthermore, several recent studies have lit a new discussion concerning the real power of physical activity on brain function. Here we aimed to clarify some of these beneficial effects, like the capacity for physical exercise to accelerate the consolidation effect of performance enhancement without additional training. Amongst the reported benefits of physical activity and exercise on brain functioning[26], is the capacity to reorganize a learned motor sequence and enhance motor performance without additional training[5] as a sleep dependent effect. A recent study[27] showed that the role of sleep on motor memory consolidation is not yet completely understood as they refute previous theories concerning the enhancement on motor sequences induced by sleep. According to the same authors, sleep does not enhance but rather stabilizes motor sequence performance. Independently on the role of sleep, over the past years several studies showed that physical activity plays an important role on the brain changes and enhancement during a training session of a motor sequence[26]. It is of paramount importance that more research be conducted in order to understand how physical activity and exercise might interfere with the consolidation of motor memories and what behavioral and biochemical changes are responsible for this. Despite the fact that we made a behavioral approach, previous investigations in neuroscience can help us to clarify our data. The enhancement of motor sequences motivated by physical exercise can be supported by several effects that occur in the brain structure during and after a physical exercise, like higher production of BDNF[28] , higher cerebral blood flow[29] and higher excitability on the primary motor cortex[13]. All the changes reported by these previous investigations that occur in the brain with physical activity can help us to better understand our behavioral data and create a global vision of what is happening in our brain while we exercise.

It is also known from previous research that after practice of a motor sequence, our brain organizes the new motor scheme in a way that our performance is enhanced approximately between 20% and 25 % after 24 hours[4]. Other studies found similar consolidation process phases with similar enhancements but right after 6 hours after the training session[30]. These studies had similar goals to our investigation, but used different protocols. The literature is still not sufficient to create a sustainable basis of knowledge. However, here we shed new light about the fact that a high intensity exercise, can render the consolidation period shorter. Our results, show that if we perform a high intensity exercise after training a new motor sequence, we will have the same performance enhancement on the motor sequence (between 20% and 25%) 1 hour after the session, that we would have several hours latter without the physical exercise. In other words, our results show a capacity to anticipate the enhancement on motor sequence task, without additional training, when associated to a high intensity physical exercise. This can be extremely important either for athletes or people going through motor recovery because it will help to re-design training plans, taking into consideration, not only the motor sequence to be learned, but also the intensity of the physical exercise to be performed, usually associated to the motor task. However, there is also some research concerning the limits of the effects of exercise intensity on cognitive performance[31]. The same authors, proposed a protocol with a Reaction Time task and with a focus on cognitive control, but can be another starting point for a detailed analysis about the relationship between physical exercise intensity and brain functions. These behavioral studies help us to understand the cortical changes made by exercise in our brain, like the research made by Gutmann and collaborators[14], where they used an EEG to describe an increase on alpha peak frequency after an intense physical exercise, but after a steady state exercise this increase would not occur.

When considering the low intensity exercise group, the measurements made 1 hour after the training session did not show better performance, and the expected enhancement only happened 24 hours after the training session as described above. These data are different

from a study made by Roig and collaborators[25], where they evaluate the effects of a single bout of physical exercise, before and after a motor learning task, and found an enhancement of performance during consolidation only 24 hours and 7 days after the training session. Their measurements made 1 hour after the training session did not show better performance compared to the training session. These
differences can be explained by different task protocols, different intensities or different types of exercise. Moreover, as we already described above, the expected enhancement on motor performance usually happens 24 hour after the training session without additional training[30]. The results are in agreement with what we found in our Rest group and Low intensity exercise group, giving more support to the thesis that the enhancement gain on the High intensity exercise group (1 hour after the training session), was motivated by the physical exercise and not just by a time period.

The understanding of these effects of exercise on brain functions, motor actions or other cognitive activities are extremely important due to the fact that physical activity can prevent cognitive decline in older adults[32], and to the best of our knowledge, we should maintain regular physical activity, in order to develop the positive effects modulated by exercise.

Together with other strategies such as mental training[33], physical exercise, at the right intensity, can be an excellent enhancer of motor learning. This approach was already suggested by Curlik and Shors[34] on a review paper where mental and physical training enhanced the process of neurogenesis in the hippocampus.

Our results shed new light on the best strategies to potentiate motor learning and brain functions that may be enhanced by physical exercise.

Methods

Participants

Seventy two neurotypical subjects (36 male and 36 Female) participated in this study. The participants were randomly assigned to one of the three groups that performed a finger tapping sequence task either in Rest (REST, n = 24 Medium Age = 25.42; SD = 2.64 years) or after an acute bout of low intensity exercise (LOW EXER, n = 24 Medium Age = 22.21; SD = 3.28 years) or after an acute bout of high intensity exercise (HIGH EXER, n = 24 Medium Age = 21.58; SD = 2.22 years). All participants were right handed and had no outstanding medical condition that might impair fine motor performance.

Procedures

Participants gave their written informed consent prior to participating in the study and received information concerning the experimental procedures. This study was conducted in accordance with the tenets of the Declaration of Helsinki (2008). The participants' performance was assessed in a Finger Tapping Sequence (FTS) task, in order to investigate motor learning, and the effect of consolidation after bouts of different physical exercise intensities. Assessment was conducted in accordance with procedures previously described[4]. The FTS task was first performed in a Training Session (T0 to T1). During this session, Baseline Performance – T0 (first time the subject executed the task) and Performance after training – T1 (average of the last 3 trials) – were assessed. Immediately after this training session, the Exercise groups performed an acute bout of physical exercise at low or high intensities, respectively. The Rest group performed no exercise after the training period, and the three groups were re-tested on the same task, 1 hour after the training session - T2, 24 hour after the training session - T3, and 7 days after the training session - T4. These delays were performed without additional training. Participants were tested in a silent and dimly lit room with the fewest distractors possible. Participants were also instructed to have a good night of sleep (7 to 9 hours) between the training session and the 24 hour period assessment as well as the 7 day period assessment. All subjects met this inclusion criteria.

Task Apparatus

The Finger Tapping Sequence task was presented on a computer and participants were seated at a distance of ± 60 cm from the computer screen. For the task, participants were instructed to tap a 5 number sequence on the computer keyboard (task described bellow). Participants were instructed to tap the sequence, as quickly and accurately as possible

Task

Finger Tapping Sequence

The learning of a motor sequence depends, in part, on the period during which subjects learn and enhance performance during practice (on-line period), and on the period during which performance continues to enhance without additional training (off-line period), during several hours or even days[35].

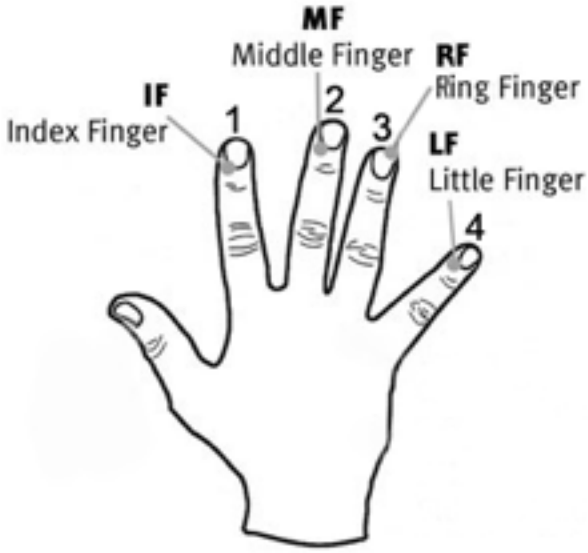

Figure 2. Digit-to-finger correspondence for the Finger Tapping Sequence task (Sequence: 4_1_3_2_4). Taken from our previous study[4].

As stated above, we followed the same research design as described in Pereira et al. (2014). All three groups were required to learn a Finger Tapping Sequence (4_1_3_2_4) by using a computer keyboard. The finger sequence corresponded to computer keys as follows: digit 1 – Index finger; digit 2 – Middle finger; digit 3 – Ring finger; digit 4 – Little finger. The participants were requested to repeat the sequence as quickly and as accurately as possible during 30 seconds, continuously without stopping even when making an error. The participants were instructed that they should perform as quickly and accurately as possible. The start and stop of each trial was given by an auditory signal cue. Performance was given by the number of correctly typed sequences. The training session consisted of twelve 30-second trials with 30-second rest periods in between trials lasting ± 12 min in total. Baseline Performance (T0) consisted on the first 30-second trial, whereas Performance After Training (T1) was given by the mean of the last 3 trials during the training session. The Consolidation Sessions (T2, T3 and T4) consisted of three 30-second trials with 30-second rest periods between trials, executed 1 hour, 24 hours and 7 days after training and without additional training. These consolidation performance scores were obtained as the result of the mean of the three 30-second trials.

Exercise

In order to assess the effects of physical exercise on the consolidation period (off-line period) of the Finger Tapping Sequence, subjects from groups HIGH EXER and LOW EXER performed a single bout of exercise on a treadmill during 12 minutes at an intensity of 85% and 70% of their Training Heart Rate after the learning session of the sequence task.

To target the Training Heart Rate (70% for Low intensity exercise and 85% for high intensity exercise) we used the Karvonen formula[36]:

$THR = ((HR_{max} - HR_{rest}) \times \%\ intensity) + HR_{rest}$

Where:

HRmax (Máximum Heart Rate): $HR_{max} = 208 - (0.7 \times age)$[37]

HR rest (Heart Rate in Rest): Measured with subjects lay-down in a quiet room, during 3 consecutive days, at the same hour of the day, with a Polar RS400.

Intensity: 70% or 85% on the Low intensity exercise group and High intensity exercise group respectively.

The 12 minutes of exercise were preceded by a warm up phase of 5 minutes in order for subjects to reach the intensities of 70% and 85%.

The treadmill grade was 0 and the velocity was controlled by the subject heart rate in order to maintain the individual target heart rate previously calculated.

The physical exercise was performed on a BH Treadmill and subjects were instructed to wear light, technical and comfortable clothes to perform the physical exercise.

Heart rate was monitored by means of a cardiofrequencimeter Polar RS400, up to 5 minutes prior to the exercise until the recovery of rest-level heart rate.

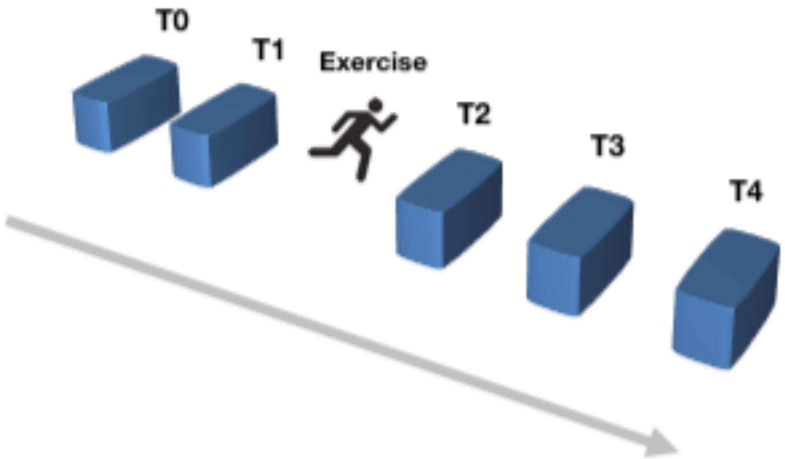

Figure 3. Time-line for different performance measures and physical exercise.

References

1. Morgan, J. A., Corrigan, F., Baune, B.. Effects of physical exercise on central nervous system functions: a review of brain region specific adaptations. *Journal of Molecular Psychiatry 3:3* (2015).

2. Dudai, Y.. The neurobiology of consolidations, or, how stable is the engram?. *Annu. Rev. Psychol.*. 55, 51-86 (2004).

3. Dehkordi, P. S., Abdoli, B., Zadeh, M. N., & Ashayeri, H.. The Time Course of off-line for Consolidation in Implicit Motor Sequence Learning in Young Adults. *Medicinski Glasnik/Medical Gazette*. 19(53) (2014).

4. Pereira, T., Castro-Caldas, A., & Abreu, A. M.. Age-related Gender Differences in Motor and Inhibitory Learning and Consolidation. *Journal of Advanced Neuroscience Research.* 1, 10-21 (2014).

5. Walker, M. P., Brakefield, T., Morgan, A., Hobson, J. A., & Stickgold, R. Practice with sleep makes perfect: Sleep dependent motor skill learning. *Neuron.* 35, 205-211 (2002).

6. Nemeth, D., Janacsek, K., Londe, Z., Ullman, M. T., Howard, D. V., & Howard Jr, J. H.. Sleep has no critical role in implicit motor sequence learning in young and old adults. *Experimental Brain Research*. 201(2), 351-358 (2010).

7. Cai, D. J., & Rickard, T. C.. Reconsidering the role of sleep for motor memory. *Behavioral neuroscience*. 123(6), 1153 (2009).

8. Albouy, G., Sterpenich, V., Vandewalle, G., Darsaud, A., Gais, S., Rauchs, G., Desseilles, M., Boly, M., Dang-Vu, T., Balteau, E., Degueldre, C., Phillips, C., Luxen, A., Maquet, P.. Interaction between hippocampal and striatal systems predicts subsequent consolidation of motor sequence memory. *PLoS One*. 8(3), e59490 (2013).

9. Pereira, T., Abreu, A. M., & Castro-Caldas, A.. Understanding Task and Expertise-Specific Motor Acquisition and Motor Memory Formation and Consolidation 1, 2, 3. *Perceptual & Motor Skills*. 117(1), 108-129 (2013).

10. Lee, I. M., Shiroma, E. J., Lobelo, F., Puska, P., Blair, S. N., Katzmarzyk, P. T., & Lancet. Physical Activity Series Working Group. Effect of physical inactivity on major non-communicable diseases worldwide: an analysis of burden of disease and life expectancy. *The Lancet*. 380(9838), 219-229 (2012).

11. Pedersen BK, Saltin B.. Evidence for prescribing exercise as therapy in chronic disease. *Scand J Med Sci Sports*. 16(Suppl 1): 3-63 (2006).

12. Berchtold NC, Castello N, Cotman CW.. Exercise and time-dependent benefits to learning and memory. *Neuroscience*. 167: 588-597 (2010).

13. Singh, Amaya M., and W. Richard Staines The Effects of Acute Aerobic Exercise on the Primary Motor Cortex. Journal of motor behavior 47.4 : 328-339. *Sports Exercise* 41: 927–934 (2015).

14. Gutmann, B., Mierau, A., Hülsdünker, T., Hildebrand, C., Przyklenk, A., Hollmann, W., & Strüder, H. K.. Effects of Physical Exercise on Individual Resting State EEG Alpha Peak Frequency. *Neural plasticity. (2015)*.

15. Thomas, A. G., Dennis, A., Bandettini, P. A., & Johansen-Berg, H.. The effects of aerobic activity on brain structure. *Frontiers in psychology.* 3 (2012).

16. Erickson KI, Voss MW, Prakash RS, Basak C, Szabo A, et al. Exercise training increases size of hippocampus and improves memory. *Proc Natl Acad Sci.* USA 108: 3017–3022 (2011).

17. Flöel, A., Ruscheweyh, R., Krüger, K., Willemer, C., Winter, B., Völker, K., Lohmann, H., Zitzmann, M., Mooren, F., Breitenstein, C., and Knecht, S.. Physical activity and memory functions: are neurotrophins and cerebral gray matter volume the missing link? *Neuroimage*. 49, 2756–2763 (2010).

18. Yarrow, J. F., White, L. J., McCoy, S. C., & Borst, S. E.. Training augments resistance exercise induced elevation of circulating brain derived neurotrophic factor (BDNF). *Neuroscience letters*. 479(2), 161-165 (2010).

19. Lambourne, K., & Tomporowski, P.. The effect of exercise-induced arousal on cognitive task performance: a meta-regression analysis. *Brain research.* 1341, 12-24 (2010).

20. Pontifex, M., Hillman, C., Fernhall, B. O., Thompson, K., & Valentini, T.. The effect of acute aerobic and resistance exercise on working memory. *Medicine and Science in Sports and Exercise.* 41(4), 927 (2009).

21. Kenney, W. L., Wilmore, J., & Costill, D.. Physiology of Sport and Exercise 6th Edition. *Human kinetics* (2015).

22. Fisher, J. P., Hartwich, D., Seifert, T., Olesen, N. D., McNulty, C. L., Nielsen, H. B., Lieshout, J., Secher, N. H.. Cerebral perfusion, oxygenation and metabolism during exercise in young and elderly individuals. *The Journal of Physiology* 591, 1859-1870 (2013)

23. Bullock, T., & Giesbrecht, B.. Acute exercise and aerobic fitness influence selective attention during visual search. *Frontiers in psychology*. 5 (2014).

24. Chu, C. H., Alderman, B. L., Wei, G. X., & Chang, Y. K.. Effects of acute aerobic exercise on motor response inhibition: An ERP study using the stop-signal task. *Journal of Sport and Health Science*. 4(1), 73-81 (2015).

25. Roig, M., Skriver, K., Lundbye-Jensen, J., Kiens, B., & Nielsen, J. B.. A single bout of exercise improves motor memory. *PlosOne*. Volume 7; Issue 9; e44594 (2012)

26. Hillman, C. H., Erickson, K. I., & Kramer, A. F.. Be smart, exercise your heart: exercise effects on brain and cognition. *Nature reviews neuroscience.* 9(1), 58-65 (2008).

27. Nettersheim, A., Hallschmid, M., Born, J., & Diekelmann, S.. The Role of Sleep in Motor Sequence Consolidation: Stabilization Rather Than Enhancement. *The Journal of Neuroscience*. *35*(17), 6696-6702 (2015).

28. Huang, T., Larsen, K. T., Ried-Larsen, M., Møller, N. C., & Andersen, L. B.. The effects of physical activity and exercise on brain-derived neurotrophic factor in healthy humans: A review. *Scandinavian journal of medicine & science in sports*, 24(1), 1-10 (2014).

29. Bullitt, E., Rahman, F. N., Smith, J. K., Kim, E., Zeng, D., Katz, L. M., and Marks, B. L.. The effect of exercise on the cerebral vasculature of healthy aged subjects as visualized by MR angiography. *AJNR Am. J. Neuroradiol*. 30, 1857–1863 (2009).

30. Walker, M. P., Brakefield, T., Seidman, J., Morgan, A., Hobson, J. A., & Stickgold, R.. Sleep and the time course of motor skill learning. *Learning & Memory. 10*(4), 275-284 (2003).

31. Davranche, Karen, Jeanick Brisswalter, and Rémi Radel. Where are the limits of the effects of exercise intensity on cognitive control? *Journal of Sport and Health Science.* 4.1 : 56-63 (2015).

32. Lista and G. Sorrentino. Biological mechanisms of physical activity in preventing cognitive decline. *Cellular and Molecular Neurobiology*. vol. 30, no. 4, pp. 493–503 (2010).

33. Gentili, R., Han, C. E., Schweighofer, N., & Papaxanthis, C.. Motor learning without doing: trial-by-trial improvement in motor performance during mental training. *Journal of neurophysiology.* 104(2), 774-783 (2010).

34. Curlik, D. M., & Shors, T. J.. Training your brain: Do mental and physical (MAP) training enhance cognition through the process of neurogenesis in the hippocampus?. *Neuropharmacology. 64*, 506-514 (2013).

35. Hotermans, C., Peigneux, P., de Noordhout, A. M., Moonen, G., & Maquet, P.. Early boost and slow consolidation in motor skill learning. *Learning & memory.* 13(5), 580-583(2006).

36. Karvonen J, Vuorimaa T. "Heart rate and exercise intensity during sports activities. Practical application". *Sports Medicine* 5 (5): 303–11(1988).

37. Tanaka H, Monahan KD, Seals DR. "Age-predicted maximal heart rate revisited". *J. Am. Coll. Cardiol.* 37 (1): 153–6 (2001).

FOURTH STUDY

Pereira, T., Abreu, A. M., & Castro-Caldas, A. (under submission). The Effects of Acute Exercise and Cardiovascular Fitness on a Motor Inhibition Task

Short Report (under submission)

The Effects of Acute Exercise and Cardiovascular Fitness on a Motor Inhibition Task

Pereira, T.[1], Abreu A. M.[3] & Castro-Caldas A.[1]

[1] *Centro de Investigação Interdisciplinar em Saúde, Universidade Católica Portuguesa, Lisbon, Portugal*

[2] *Universidade Europeia, Laureate International Universities, Lisbon, Portugal*

Abstract

Physical exercise is held to be one of the most important strategies to improve motor cognition and to reduce executive function decline with aging. However, it is far from clear what type of physical exercise and what intensity or regularity might produce the most efficient results. In this study we aim to investigate the effects of acute physical exercise and cardiovascular fitness on the inhibition performance of a motor task through a go no go paradigm. In order to investigate the impact of cardiovascular fitness in task performance, we used VO2max, that reflects the long-term effects of aerobic training in metabolic systems and consequently on the brain. We used this indicator to separate the two groups of subjects. The first group had a higher cardiovascular fitness (VO2max above 50 ml/kg/min) and the second had a lower cardiovascular fitness (VO2max bellow 50 ml/kg/min). For the acute condition, we asked the subjects from both groups to perform a 12-minute run on a treadmill at 75% of their maximum training capacity.Acute exercise had no effect on both groups, however, higher cardiovascular fitness led to better results on both conditions - in rest and following acute exercise. Acute physical exercise *per se* cannot change our capacity to react to a go/no-go task, however, when chronic, physical activity comes into play, leading to higher VO2max, performance in an inhibition go/no-go task is enhanced.

Keywords: Physical Exercise; Cardiovascular Fitness; Motor Inhibition; Reaction Time

Introduction

The decision-making process is sometimes dependent on the inhibition of some motor action in order to promote another executive function. This mechanism is important for sport activities, but also in many of our daily motor decisions that become compromised with the reduction of our cognition with aging (for review see Bherer et al., 2013). The understanding of the best strategies to optimize our reaction to a stimuli will help us optimize the decision-making process and, according to previous research, physical activity is one of such strategy that aid in the enhancement of reaction time for the execution of a motor task (Chu et al., 2015). We have shed new light on how motor inhibition and reaction time is modulated across the life-span (Pereira et al., 2014). Here, we aim to investigate the effects of acute physical exercise and fitness level (VO2max capacity) on the reaction time of a go/no-go task.

The unconscious process of decision-making is very important in sports and many other daily tasks (Kida et al., 2005). Physical activity can play an important role in this mechanism but results on the effects of physical exercise on the decision making process are still unclear. Research on the effects of aerobic exercise on executive functions has, thus far, not showed consistent results (for review see Guiney & Machado, 2013). Most studies have considered the acute effects of physical exercise as proof that exercise helps to maintain and improve cognitive performance throughout the lifespan (Akatsuka et al., 2015). Moreover, enhancements in performance due to acute physical exercise have been explained by higher arousal and modulation of biochemical mechanisms like cortisol (Tsai et al., 2014). Although important, the acute effects of exercise do not represent the long-term modifications in brain structure and function. Physical exercise affects brain cognition (Hillman et al., 2008) through changes on some brain structures like hippocampus, cerebellum and motor cortex (Thomas et al., 2012). Experts in Physical exercise, such as athletes, for example have better performances on a reaction-time task when compared with non-athletes (Pereira et al., 2013). Difference on a go no go task reaction time were found in athletes from different sports showing differences in the capacity to inhibit a motor action. (Kida et al., 2005), and also in people with different fitness levels (Stroth et al., 2009). However, another study found no significant differences between participants with different fitness levels or fencing expertise when considering reaction time in a go/no-go task (Chan et al., 2011). Based on the assumption that cardiovascular fitness is very telling when considering the chronic effect of physical exercise, it is probable that higher fitness levels represent a longer exercise effect on muscles, energy systems and, consequently, on the brain. Thus, and considering the reported inconsistencies, here we propose to analyze the effects of acute physical exercise and cardiovascular fitness on the performance of a Go/No-Go task.

Methods

Forty-eight neurotypical participants were divided into two groups: G1 presented higher cardiovascular fitness (VO2max > 50 ml/kg/min) (aged M = 24.82 years; SD = 2.69 years) and G2 presented lower cardiovascular fitness (VO2max < 50 ml/kg/min) (aged M = 25.31 years; SD = 2.50 years). The participants were active people (between 2 and 5 sessions of exercise per week) recruited from a Portuguese university. All participants were right handed and had no medical condition that could compromise the execution of a Go/No-Go task. The VO2max (Maximum Aerobic Capacity) was measured one week before, and was obtained on a treadmill with a COSMED Fitmate PRO and the mean results are described on table 1.

Participants from both groups (VO2max > 50 ml/kg/min and VO2max < 50 ml/kg/min) performed a single bout of exercise on a treadmill during 12 minutes at an intensity of 75% of the Training Heart Rate, calculated with the Tanaka Formula (Tanaka et al., 2001). Immediately after the exercise, participants were asked to perform a Go/No-Go task. The Go/No-Go task was presented on a computer screen (how many inches?) and consisted on four arrow types (red left and right and green left and right) that were presented randomly for 1000 milliseconds interspersed with fixation crosses. Participants were instructed to press the right mouse button in response to the right green arrow; the left mouse button in response to the left green arrow and to refrain from pressing any button in the presence of any of the two red arrows. The experiment included twelve 60-trial blocks (1 trial = 1 arrow) with 30 sec rest periods between blocks. Before the task, the participants were notified that 75% of the trials were go trials and the remaining 25% consisted on no-go trials, thereby eliciting a covert tendency to make a go response. This procedure was effective in increasing inhibitory demands (Ciesielski, Harris, & Coffer, 2004).

Results

Speed and accuracy were integrated in one overall index of performance (Inverse Efficiency Score, IES) by dividing, for each subject, the mean correct reaction time by the percentage of correct responses. The IES was introduced by Townsend and Ashby (1983) to control the speed–accuracy trade-off effects, as it combines accuracy and reaction times in a single measure. Worse overall performance is given by higher scores.

The merged IESs of both groups were entered into an univariate ANOVA and we did not find a significant effect of exercise on the IES score ($F(1,46) = 1.925$, $p = 0.172$). However, when we compared both groups with different cardiovascular fitness levels (high and low), the group with a higher VO2max had better results in both conditions. G1, the higher VO2max group revealed better IES during rest ($F(1,46) = 40.978$, $p = 0.001$) and after acute exercise ($F(1,46) = 23.722$, $p = 0.001$). Mean values for G1 during rest were (368 milliseconds SD = 30.04) compared with G2, the group with a lower VO2max (433 milliseconds SE = 39.65). This difference between the two groups remained robust after a bout of acute physical exercise wherein the higher cardiovascular fitness group (G1) presented better performance given by IES (384 milliseconds SD = 47.85) when compared with G2 - the lower cardiovascular fitness group (453 milliseconds SD = 50.27).

	VO2max (ml/kg/min)		**IES Rest (milliseconds)**		**IES Exer (milliseconds)**	
	Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**
> 50 ml/kg/min	**60**	**6.95**	**368**	**30.04**	**384**	**47.85**
< 50 ml/kg/min	**37**	**7.91**	**433**	**39.65**	**453**	**50.27**

Table 1. Descriptive Statistics. Mean and standard deviation values for VO2max in ml/kg/min and for IESs in milliseconds in Rest and Exercise conditions.

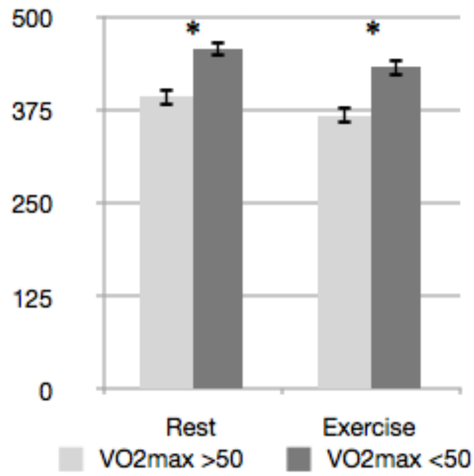

Figure 1. Performance of G1 and G2 in the Go/No-Go task. Performance for IES consists on the ratio between the mean RT and the proportion of correct responses obtained during the 60 trials. Bars represent the mean of IES. *Indicates significant comparisons ($p < 0.001$).

Discussion

The aim of this study was to investigate the effects of acute physical exercise and cardiovascular fitness levels on inhibitory control - assessed via performance on a Go/No-go task in active young adults. Despite a small tendency to reduce response times in both groups, after a bout of acute physical exercise, our results did not show a significant difference between the rest and exercise conditions. A recent investigation found an increase of the amplitude on the no-go component, after acute aerobic exercise, but did not find any changes on the go component (Akatsuka et al., 2015), suggesting that physical exercise acts only on the inhibition process. However, we found a significant main effect of group The general performance given by the IESs from the group with the VO2max above 50 ml/kg/min (G1) outperformed G2 (VO2max below 50 ml/kg/min). We suggest that chronic exercise may have a positive effect on reaction time and accuracy. The effects of acute physical exercise on brain structure are limited in time and they do not represent the long-term effects of physical exercise (Hillman et al., 2008). On the other hand, continued performance of an aerobic training plan, can lead to changes in brain structure and function such as in the hippocampus, gray matter, vasculature, brain plasticity and biochemical changes (Thomas et al., 2012). Such changes may underly our results wherein acute exercise did not change performance in a Go/No-Go task, but when comparing the high and low cardiovascular fitness groups, better performance was obtained by the fittest group which is in accordance with similar data stemming from a recent research that compared highly talented soccer players with amateur soccer players. Better inhibition and reaction times were obtained by the highly talented (Verburgh et al., 2014). In tandem with our own results, this study also showed the effects of chronic physical exercise on brain executive functions. However, it is important to refer that the participants in our research were active subjects. However, we did not consider the sports or physical activity they used to practice, since we used VO2max as a reference. A highly talented soccer player has, not only a higher VO2max, but also more training hours on specific motor schemes that might also aid performance in the inhibitory task.

Future studies may demonstrate the potential of different types of physical exercise and analyze different sport activities as a complementary tool to reduce neurodegenerative diseases and optimize performance of athletes. Our results clearly state that physical exercise should be performed as a long-term activity in order to potentiate a better reaction to a decision making on brain executive functions.

References

Akatsuka, K., Yamashiro, K., Nakazawa, S., Mitsuzono, R., & Maruyama, A. (2015). Acute aerobic exercise influences the inhibitory process in the go/no-go task in humans. *Neuroscience Letters*, 600, 80-84.

Bherer, L., Erickson, K. I., & Liu-Ambrose, T. (2013). A review of the effects of physical activity and exercise on cognitive and brain functions in older adults. *Journal of aging research*, 2013.

Chan, J. S., Wong, A. C., Liu, Y., Yu, J., & Yan, J. H. (2011). Fencing expertise and physical fitness enhance action inhibition. *Psychology of Sport and Exercise*, 12(5), 509-514.

Chu, C. H., Alderman, B. L., Wei, G. X., & Chang, Y. K. (2015). Effects of acute aerobic exercise on motor response inhibition: An ERP study using the stop-signal task. *Journal of Sport and Health Science*, 4(1), 73-81.

Ciesielski, K. T., Harris, R. J., & Coffer, L. F. (2004). Posterior brain ERP patterns related to the go/no-go task in children. *Psychophysiology*, 41, 882e892.

Guiney, H., & Machado, L. (2013). Benefits of regular aerobic exercise for executive functioning in healthy populations. *Psychonomic Bulletin & Review*, 20(1), 73-86.

Hillman, C. H., Erickson, K. I., & Kramer, A. F. (2008). Be smart, exercise your heart: exercise effects on brain and cognition. *Nature reviews neuroscience*, 9(1), 58-65.

Kida, N., Oda, S., & Matsumura, M. (2005). Intensive baseball practice improves the go/no-go reaction time, but not the simple reaction time. *Cognitive Brain Research*, 22, 257e264.

Pereira, T., Abreu, A. M., & Castro-Caldas, A. (2013). Understanding Task-and Expertise-Specific Motor Acquisition and Motor Memory Formation and Consolidation. *Perceptual & Motor Skills*, 117(1), 108-129.

Pereira, T., Castro-Caldas, A., & Abreu, A. M. (2014). Age-related Gender Differences in Motor and Inhibitory Learning and Consolidation. *Journal of Advanced Neuroscience Research*, 1, 10-21.

Stroth, S., Kubesch, S., Dieterle, K., Ruchsow, M., Heim, R., & Kiefer, M. (2009). Physical fitness, but not acute exercise modulates event-related potential indices for executive control in healthy adolescents. *Brain Research*, 1269, 114e124.

Tanaka H, Monahan KD, Seals DR (2001). "Age-predicted maximal heart rate revisited". *J. Am. Coll. Cardiol*. 37 (1): 153–6.

Thomas, A. G., Dennis, A., Bandettini, P. A., & Johansen-Berg, H. (2012). The effects of aerobic activity on brain structure. *Frontiers in psychology*, 3.

Townsend JT, Ashby FG. Stochastic modeling of elementary psychological processes. Cambridge: *Cambridge University Press*; 1983.

Tsai, C. L., Wang, C. H., Pan, C. Y., Chen, F. C., Huang, T. H., & Chou, F. Y. (2014). Executive function and endocrinological responses to acute resistance exercise. *Frontiers in Behavioral Neuroscience*, 8, 262

Verburgh, L., Scherder, E. J., van Lange, P. A., & Oosterlaan, J. (2014). Executive functioning in highly talented soccer players. *PloS One*, 9(3), e91254

FINAL DISCUSSION

Nowadays, in high performance sports, the difference between winning and not winning a medal is so small that athletes and coaches are looking for the ultimate training programs and methodologies that will make them reach the podium. High performance achievements in sports are not only driven by muscles, bones and ligaments, but also by the ability to form and recall the most efficient motor memories (Kantak & Winstein, 2012). Motor memory formation and recall can be optimized if we understand the neural underpinnings of these processes. In order to achieve such understanding we must link neuroscience and sports in a way that will afford the achievement of better results by high performance athletes. Hence, high performance training plans should be based on a research methodology where brain activity and motor performance are deeply intertwined and where both data from brain molecular structural changes and behavioral changes are analyzed. The gap between these two areas of research - molecular neuroscience and behavioral neuroscience is being reduced in tandem with the latest advances in this field such as those showing a clear correlation between the models of anatomical networks and the observed behavior (for review see Zatorre et al., 2012). An example of these advances is the use of Diffusion Tensor Imaging techniques to study the influence of emotions on motor behavior (Grazes et. al., 2014) that help us to connect different data and visualize the motor learning and consolidation processes from an holistic point of view. We state this having in mind that, it is very difficult for coaches, physiotherapists or other professionals that, to deal with motor improvement and/or recovery, it's fundamental to understand and breakdown a motor movement into a molecular and behavioral perspective. Moreover, to build new training plans based on the latest neuroscience and physical exercise research, capable of changing today’s high performance results and simultaneously accelerate the recovery of people with motor disabilities, different studies need to be integrated into a series of dynamic models that might serve as the basis of these new training plans. However, before we are able to do this, we must understand the differences in performance across motor tasks and it’s influence on brain activity, due to task specificities.

Similarly to brain research based on deviations from the normal population that allow us to better understand the function of a normal brain, we used, in our first study, a sample of athletes that also constitute a deviation from normality, albeit with a higher motor performance and a regular practice of physical exercise. This allowed us to understand how chronic physical exercise might interfere with learning and consolidation of motor tasks. Studying athletes or people with a high level of motor activity allows us to understand the limits and benefits of physical exercise on brain functions. In addition, this information should be related with the benefits of physical exercise, not only in adults, but also across the life-span. The importance of this scope of research across different ages stems from previous knowledge sustaining that the brain functions differently across these older (Bherer et al., 2013) or young (Verburgh et al., 2013) populations and thus, similar physical exercise should also have different effects on brain structure and function according to age or different levels of cardiovascular fitness. Following the same line of research, there are people who were exposed to chronic physical exercise (e.g., athletes) or people who's physical fitness is above average and have suffered functional and structural changes to the brain (Yarrow et al., 2009) that might facilitate learning and consolidation of new motor skills.

One of our goals, as humans, is to improve and develop performance and motor tasks are no exception. Despite the fact that we tend to use less and less our motor system, due to modern technologies, the fact is that the human body evolved to improve with training (O'Keefe et al., 2011). Since success, in our society, is more dependent on cognitive improvements than on motor performance (O'Keefe et al., 2011), we tend to train cognitive tasks more and forget our motor system. Movement is one of the first interactions we have with the environment by the representation of actions that will allow us to proceed with our motor development (Burzi et al., 2015) and these interactions between our perception and adaptation to the environment continues until an older age (Huang & Ahmed, 2014). Thus, the motor system is one of the bases for most of our everyday tasks and it slows down with age. It is hence paramount to understand not just how such a decrease occurs, but also how the quality of life across the aging population might be improved despite this decrease in motor action. Independently of our age we cannot dissociate the relationship between the positive effects of physical exercise on brain structure (Thomas et al., 2012) and cognitive processes (Hötting, K., & Röder, B., 2013) During the last years, research has demonstrated that physical exercise can have an extremely important role improving brain activity and functions (Morgan et al., 2015). The belief that regular physical exercise might improve the cardiovascular system, the muscular function and other collateral improvements related to an increase in global cellular and molecular metabolism (Neufer et al., 2015), is very well established and integrated on general population knowledge. Nevertheless, new insights in neuroscience and physical exercise allow us to amplify this perspective even further by realizing that some of the changes that occur in the body that result from physical exercise (for review see Reiner et al., 2013) are accompanied by improvements on brain structure and functions (Thomas et al., 2012). It is not our goal to isolate the importance of physical exercise on brain cognitive processes, but to better understand how physical exercise can serve as a leverage on the process of motor learning and consolidation. Before we have a clear understanding of how the brain and its inner processes can be modulated by physical exercise, we need to clarify the effects of different tasks, different time periods across life, different exercise intensities and different fitness levels. Our line of research tried to shed new light on these topics and brought some results that might help to optimize training plans on athletes or on people recovering from a motor disability. In summary, we showed that physical activity cannot be generalized as training plans are not reliably designed to be developed with different populations, exercises or tasks and this, was one of our main goals to achieve with the four studies we presented. With our research we were able to show that physical activity can enhance differences on motor performance when learning a new motor task (and when practiced for long periods) when we compared with athletes and non-athletes (Pereira et al., 2013).

Higher performance resulting from the off-line period, can be different between tasks, but it also changes across life (Pereira et al., 2014). This means that, during our life span we can have different consolidation processes resulting in more or less enhancement of motor performance. These results showed us that older people were not able to enhance their motor performance on a sequence task, during the consolidation period and children have similar performances to adults. Knowing that motor tasks and physical exercise can play an important role on memory learning and consolidation (as described above in our data), it is important, for sports and clinical recovery, to understand the relationship between the difficulty of older adults, to enhance motor sequences during the off-line period of consolidation and the ease with which young adults can learn and consolidate new tasks. Crucially, the fact that children are not the better age group when learning and consolidating a new motor task, should lead to more care when setting up motor learning plans for children, in a way that learning and consolidation might be optimized.

It is also important to understand that motor skill learning is always dependent on some physical activity and most of our daily motor tasks can change with our physical fitness level or with the physical exercise we are performing during task learning. In our third study (Pereira et al., submitted to Scientific Reports) where we tested the influence of a single bout of exercise on motor memory consolidation, we found evidence that motor memory consolidation is a very dynamic process that can be influenced by exercise. This research showed that physical exercise could accelerate the process of consolidation of a motor sequence in a high intensity exercise condition, but not in the lower intensity exercise condition. A recent meta-analytic review with a different protocol and task from those we used, found no differences for both high intensity and low intensity exercises on the increase of speed cognitive functioning (McMorris & Hale 2015). Despite the fact that, in our research we were analyzing different data compared to the aforementioned study (motor memory consolidation in our study and cognitive functioning in McMorris and Hale’s study), the differences in findings is something to consider in further investigations taking into account that different exercise intensities have different influences on the consolidation of a motor task. For a practical application we know that every motor task we learn is accompanied by some kind of physical activity and its intensity must be controlled together with the training of the task to ensure that we optimize the learning process.

In addition to this, the results we had in our fourth study brought us more evidence that chronic physical activity can enhance a Go No Go task, when we people that perform regular physical activity with people that have a lower chronic physical activity. These results are extremely important to complement previous investigations on physical activity, cognition and brain functions in older adults (Bherer et al., 2013). Mostly to understand that, despite the fact that physical activity might have a positive effect on our brain functions, independently of age, on the other hand, the sooner we start practicing physical exercise, the better. According to our data, the long term effects of physical exercise can improve a Go No Go task. However, we are far from understanding what type of exercise, frequency or intensity are the most efficient to improve each specific task or function that we might want to maintain during our life span.

With the data we collected so far and following this line of research, we will be able to built better training plans and optimize the learning and consolidation of a motor task, integrating different variables that most of the times are not considered, like different tasks, age, exercise or fitness levels.

Our results show that a bout of high intensity physical exercise might anticipate performance enhancement in young adults and this sheds important new light on the consolidation process in older adults and a possible strategy to potentiate consolidation in older adults. In this line, the same protocols (putting together motor memory consolidation and physical exercise) can be adapted to different age groups and different motor expertise groups (Athletes and Non-Athletes). This relationship is not new but with modern neuroscientific methods available, such as fMRI, TMS or EEG, it will be easier to develop integrated protocols that can give us detailed information about brain activity, networks and motor behavior when attending to a specific motor task.

Our research will help develop training plans and strategies, based on a wide scope of relationships between brain activity and motor performance, allowing the integration of this knowledge for a higher quality of life.

As our population is aging (Pordata, 2016), we are living longer and, naturally, we need to find strategies to deal with motor and neurodegenerative diseases that have also been increasing (Pordata, 2016). During the last decade we have witnessed an increase in some lifestyle habits that can be determinant for slowing down the rate of cognitive decline and preventing dementia: a socially integrated network, cognitive leisure activity, and regular physical activity (Fratiglioni et al., 2004). However, motor and physical activity is probably the most neglected of these factors. According to what we have seen over the last years, this reality might be changing, based on the results from several studies that point to physical activity and exercise as one of the most important strategies to avoid cognitive decline and preventing neurodegenerative diseases (Hilman et al., 2008).

What we are now is the result of an evolutionary process that brought together brain and muscle physiology to work together and coordinate responses to our daily challenges in order to fight for survival. We no longer practice as much physical activity as we should for a better brain development (Hilman et al., 2008) and it is extremely important to create exercise motivation and new habits for our society to experience better brain development and healthy aging.

The human brain tends to be efficient and economic with the development of neural networks (Sporns, 2011), i.e., the energy cost is reduced to a minimum required for an efficient metabolism. However, we must not forget the human body is the only known machine that will be more efficient with practice and time. And even with the great number of studies coming out in recent years, focusing on this topic, we are still far from understanding the complex principles of motor learning and consolidation. The protocols and instruments we have available just enable us to scratch the surface of what our brain is capable of.

FINAL CONCLUSIONS

- Different motor tasks underlie different consolidation processes.
- Athletes showed a more efficient acquisition of novel motor tasks, perhaps because the new tasks were anchored on previously acquired motor schemes.
- The consolidation process showed similar performance improvements between athletes and non-athletes.
- Independently of being an athlete or not, when we investigate motor sequence task learning and consolidation performance, between different age groups, we found that Seniors were the only group that is not able to improve their performance after training during the off-line period (consolidation).
- Once again, when comparing different age groups, the consolidation mechanism was shown to be task-specific given by off-line gains on motor performance associated to a finger tapping sequence task but not to a Go No Go task.
- Overall performance to react to a Go No Go task, can be differently modulated by sex, according to age group, as we found differences between men and women in all age groups, except on children.
- High intensity physical exercise accelerates the off-line gains of performance on a motor sequence task. These gains were registered only 1 hour after the training session compared with the off-line gains obtained 24 hours after training on the low intensity exercise and rest groups.
- These off-line gains improved by high intensity physical exercise are maintained 7 days after the training session.
- Acute physical exercise had no effect on rest and exercise conditions. However, when we look at the higher cardiovascular fitness group, performance on the Go No Go task in enhanced from rest to the exercise condition.
- Motor learning and consolidation are dependent on different ages, tasks or physical exercise and these variables must be considered when we design a training plan, in order to optimize the process and results.

FUTURE RESEARCH

- Understand the relationship between the difficulty of older adults, in enhancing a motor sequence during the off-line period of consolidation and physical exercise.
- Use different physical exercise intensities to analyze learning and consolidation of a motor task across the life-span.
- Enhance the scope of tasks to be tested and understand how they change motor performance across different groups.
- Different exercise intensities should be investigated in order to understand their effect on learning and consolidation of a motor task
- Study the impact of acute physical exercise, like in our fourth study, but introduce the motor training session before the bout of physical exercise, together with other exercise intensities.
- Different sport activities should also be considered to investigate how they can optimize learning and consolidation, reduce neurodegenerative diseases and leverage athlete training.

REFERENCES

Abel, T., Havekes, R., Saletin, J. M., & Walker, M. P. (2013). Sleep, plasticity and memory from molecules to whole-brain networks. Current biology, 23(17), R774-R788.

Ahlskog, J. E., Geda, Y. E., Graff-Radford, N. R., & Petersen, R. C. (2011). Physical exercise as a preventive or disease-modifying treatment of dementia and brain aging. *In Mayo Clinic Proceedings* 86, 9, 876-884.

Albouy, G., Sterpenich, V., Vandewalle, G., Darsaud, A., Gais, S., Rauchs, G., Desseilles, M., Boly, M., Dang-Vu, T., Balteau, E., Degueldre, C., Phillips, C., Luxen, A., Maquet, P.. (2013). Interaction between hippocampal and striatal systems predicts subsequent consolidation of motor sequence memory. *PLoS One*, 8(3), e59490.

Bherer, L., Erickson, K. I., & Liu-Ambrose, T. (2013). A review of the effects of physical activity and exercise on cognitive and brain functions in older adults. *Journal of aging research*, 2013.

Boutin, A., Badets, A., Salesse, R. N., Fries, U., Panzer, S., Blandin, Y. (2012) Practice makes transfer of motor skills imperfect. *Psychological research* 76.5: 611-625.

Burzi, V., Marchi, V., Boyd, R. N., Mazziotti, R., Moscarelli, M., Sgherri, G., Teald G., Cioni, G. & Guzzetta, A. (2015). Brain representation of action observation in human infants. *Developmental Medicine & Child Neurology*, 57(s2), 26-30.

Cai, D. J., & Rickard, T. C. (2009). Reconsidering the role of sleep for motor memory. *Behavioral neuroscience*, 123(6), 1153.

Chu, C. H., Alderman, B. L., Wei, G. X., & Chang, Y. K. (2015). Effects of acute aerobic exercise on motor response inhibition: An ERP study using the stop-signal task. *Journal of Sport and Health Science*, 4(1), 73-81.

Cross, E. S., Schmitt, P. J., & Grafton, S. T. (2007). Neural substrates of contextual interference during motor learning support a model of active preparation. *Journal of Cognitive Neuroscience*, 19(11), 1854-1871.

Dayan, E., & Cohen, L. G. (2011). Neuroplasticity subserving motor skill learning. *Neuron*, 72(3), 443-454.

Debarnot, U., Valenza, G., Champely, S., Scilingo, E. P., De Rossi, D., & Guillot, A. (2011). Motor imagery effectiveness for mirror reversed movements. *Cognitive, Affective, & Behavioral Neuroscience*, 11(1), 22-31.

Debas, K., Carrier, J., Orban, P., Barakat, M., Lungu, O., Vandewalle, G., Tahar, A. H., Bellec, P., Karni, A., Ungerleider, L. G., Benali, H., & Doyon, J. (2010). Brain plasticity related to the consolidation of motor sequence learning and motor adaptation. *Proceedings of the National Academy of Sciences*, 107(41), 17839-17844.

Dorfberger, S., Adi-Japha, E., & Karni, A. (2007). Reduced susceptibility to interference in the consolidation of motor memory before adolescence. *PLoS One*, 2(2), e240.

Doyon, J., and Benali, H. (2005). Reorganization and plasticity in the adult brain during learning of motor skills. *Current Opinion in Neurobiology*. 15, 161–167.

Doyon, J., Bellec, P., Amsel, R., Penhune, V., Monchi, O., Carrier, J., Lehéricy, S. & Benali, H. (2009). Contributions of the basal ganglia and functionally related brain structures to motor learning. *Behavioral Brain Research*, 199(1), 61-75.

Dudai, Y. (2004). The neurobiology of consolidations, or, how stable is the engram?. *Annu. Rev. Psychol*., 55, 51-86.

Fischer, S., Nitschke, M. F., Melchert, U. H., Erdmann C., Born, J. (2005). Motor memory consolidation in sleep shapes more effective neuronal representations. *Journal of Neuroscience* 25:11248–11255.

Gambetta, V. (2007). Athletic development: The art & science of functional sports conditioning. *New World Library*.

Grezes, J., Valabregue, R., Gholipour, B., & Chevallier, C. (2014). A direct amygdala–motor pathway for emotional displays to influence action: A diffusion tensor imaging study. *Human Brain Mapping*, 35(12), 5974-5983.

Guimaraes, T. T., da Costa, B. M., Cerqueira, L. S., Serdeiro, A. D. C. A., Pompeu, F. A. M. S., de Moraes, H. S., Santos, T. M. & Deslandes, A. C. (2015). Acute effect of different patterns of exercise on mood, anxiety and cortical activity. *Archives of Neuroscience*, 2(1).

Gutmann, Boris, et al. Effects of Physical Exercise on Individual Resting State EEG Alpha Peak Frequency. *Neural Plasticity* (2015).

Hillman, C. H., Kirk, I. E., & Arthur F. K. (2008). Be smart, exercise your heart: exercise effects on brain and cognition. *Nature Reviews Neuroscience* 9(1): 58-65.

Hötting, K., & Röder, B. (2013). Beneficial effects of physical exercise on neuroplasticity and cognition. *Neuroscience & Biobehavioral Reviews*, 37(9), 2243-2257.

Huang, H. J., & Ahmed, A. A. (2014). Older adults learn less, but still reduce metabolic cost, during motor adaptation. *Journal of Neurophysiology*, 111(1), 135-144.

Kantak, S. S., & Winstein, C. J. (2012). Learning–performance distinction and memory processes for motor skills: A focused review and perspective. *Behavioral Brain Research*, 228(1), 219-231.

Krakauer, J. W., & Shadmehr, R. (2006). Consolidation of motor memory. *Trends in Neurosciences*, 29(1), 58-64.

L. Fratiglioni, L., Paillard-Borg, S. & Winblad, B. (2004). An active and socially integrated lifestyle in late life might protect against dementia. *The Lancet Neurology* 3(6) 343–353.

Lambourne, K., Audiffren, M., & Tomporowski, P. D. (2010). Effects of acute exercise on sensory and executive processing tasks. *Med Sci Sports Exercise*, 42(7), 1396-1402.

Lashley, K. S. (1988). In search of the engram. *In Physiological mechanisms in animal behavior,* vol. 4 (Society of Experimental Biology Symposium). Cambridge University Press.

McMorris, T., & Hale, B. J. (2015). Is there an acute exercise-induced physiological/ biochemical threshold which triggers increased speed of cognitive functioning? A meta-analytic investigation. *Journal of Sport and Health Science*, 4(1), 4-13.

Morgan, J. A., Corrigan, F., & Baune, B. T. (2015). Effects of physical exercise on central nervous system functions: a review of brain region specific adaptations. *Journal of molecular psychiatry*, 3(1), 1.

Neufer, P. D., Bamman, M. M., Muoio, D. M., Bouchard, C., Cooper, D. M., Goodpaster, B. H., Both, F. W., Kohrt, W. M., Gerszten, R. E., Mattson, M. P., Hepple, R. T., Kraus, W. E., Reid, M. B., Bodine, S. C., Jakicic, J.M., Fleg, J. L., Williams, J. P., Joseph, L., Evans, M., Maruvada, P., Rodgers, M., Roary, M., Boyce, A. T., Drugan, J. K., Koenig, J. I., Ingraham, R. H., Krotoski, D., Garcia-Cazarin, M., McGowan,J. A. Laughlin, M. R. (2015). Understanding the cellular and molecular mechanisms of physical activity-induced health benefits. *Cell metabolism*, 22(1), 4-11.

O'Keefe, J. H., Vogel, R., Lavie, C. J., & Cordain, L. (2011). Exercise like a hunter-gatherer: a prescription for organic physical fitness. *Progress in cardiovascular diseases*, 53(6), 471-479.

Panzer, S., Gruetzmacher, N., Fries, U., Krueger, M., & Shea, C. H. (2011). Age-related effects in interlimb practice on coding complex movement sequences. *Human Movement Science*, 30(3), 459-474.

Pereira, T., Abreu, A. M., & Castro-Caldas, A. (2013). Understanding task-and expertise-specific motor acquisition and motor memory formation and consolidation 1, 2, 3. *Perceptual & Motor Skills*, 117(1), 108-129.

Petersen, T. H., Willerslev-Olsen, M., Conway, B. A., & Nielsen, J. B. (2012). The motor cortex drives the muscles during walk- ing in human subjects. *Journal of Physiology*, 590, 2443–2452.

PORDATA (2016). Saldos populcionais anuais: total, natural e migratório - Portugal. Retrieved August 3rd, 2016 from *http://www.pordata.pt/Portugal/Saldos+populacionais+anuais+total++natural+e+migratório-657*

Quaney, B. M., Boyd, L. A., McDowd, J. M., Zahner, L. H., He, J., Mayo, M. S., & Macko, R. F. (2009). Aerobic exercise improves cognition and motor function poststroke. *Neurorehabilitation and Neural Repair*.

Reiner, M., Niermann, C., Jekauc, D., & Woll, A. (2013). Long-term health benefits of physical activity–a systematic review of longitudinal studies. *BMC public health*, 13(1), 1.

Robergs, R. A., Ghiasvand, F., & Parker, D. (2004). Biochemistry of exercise-induced metabolic acidosis. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 287(3), R502-R516.

Sporns, O. (2011). The non-random brain: efficiency, economy, and complex dynamics. *Frontiers in computational neuroscience*, 5.

Thomas, A. G., Dennis, A., Bandettini, P. A., & Johansen-Berg, H. (2012). The effects of aerobic activity on brain structure. *Frontiers in Psychology*, 3.

Verburgh, L., Königs, M., Scherder, E. J., & Oosterlaan, J. (2013). Physical exercise and executive functions in preadolescent children, adolescents and young adults: a meta-analysis. *British Journal of Sports Medicine*, bjsports-2012.

Voss, M. W., Nagamatsu, L. S., Liu-Ambrose, T., & Kramer, A. F. (2011). Exercise, brain, and cognition across the life span. *Journal of Applied Physiology*, 111(5), 1505-1513.

Wagner, M. J. & Smith, M. A. (2008). Shared internal models for feedforward and feedback control. *Journal of Neuroscience*. 28, 10663–10673.

Walker, M. P. (2005). A refined model of sleep and the time course of memory formation. *Behavioral and Brain Sciences*, 28(01), 51-64.

Yarrow, K., Brown, P., & Krakauer, J. W. (2009). Inside the brain of an elite athlete: the neural processes that support high achievement in sports. *Nature Reviews Neuroscience*, 10(8), 585-596.

Zatorre, R. J., Fields, R. D., & Johansen-Berg, H. (2012). Plasticity in gray and white: neuroimaging changes in brain structure during learning. *Nature neuroscience*, 15(4), 528-536.